Movement patterns of African elephants (*Loxodonta africana,* Blumenbach) in a seasonally variable ecosystem in south-eastern Chad

Zanne Claire Labuschagne

17th February 2014

Submitted in partial fulfilment of the requirements for the degree of
Masters of Science in Conservation Biology

Supervisors:

Professor David, H. M. Cumming and Professor Graeme, S. Cumming

Percy FitzPatrick Institutute of African Ornithology
University of Cape Town
Rondebosch, 7701
South Africa,
e-mail: zannelab@gmail.com

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Plagiarism declaration

I know that plagiarism is wrong. Plagiarism is using another's work and to pretend that it is one's own. I have used the Journal of Animal Ecology as the convention for citation and referencing. Each significant contribution to, and quotation in, this project from the work, or works of other people, has been attributed, cited and referenced. This project is my own work. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work. I acknowledge that copying someone else's work, or parts of it, is wrong, and declare that this is my own work.

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Acknowledgements

I am very grateful to African Parks and the Chadian Ministry of Environment and Fishery Resources in Zakouma National Park for providing the data analysed in this study as well as much information about the situation on the ground in Zakouma. I am also very grateful to Professor David Cumming of the Universities of Zimbabwe and Cape Town as well as Professor Graeme Cumming of the FitzPatrick Institute of African Ornithology for agreeing to take on the project and for their guidance, insights and comments on the write-up. I am grateful to Doctor M. Dolmia for generously allowing the use of data collected by him and his team ten years ago. Thanks to my parents, Rian and Lorna Labuschagne, two of my conservation heroes, for giving me the opportunity to do such an interesting project, for providing information and insights into the situation in Zakouma, and for the constant support during the past six months. Finally, thanks to the Conservation Biology class of 2013, for making long hours in the lab enjoyable.

Abstract

African elephant (*Loxodonta africana)* range and numbers have declined over the past century as a result of increasing human populations, agricultural development, and illegal hunting for ivory. Understanding the dynamics of wide-ranging animal migrations is important for the conservation of these species and their habitats in a rapidly changing world. The study of movement has greatly advanced in the past few decades and novel approaches for characterizing and interpreting complex movement data, predominantly collected through telemetry, have emerged. The Zakouma National Park elephant population has declined dramatically over the past ten years due to rampant ivory poaching. Several elephants in this population were fitted with satellite collars between 2011 and 2012. The telemetry data collected from these animals, in combination with data collected from the same population ten years earlier, provides spatio-temporal movement data from before and after a period of severe poaching. Broad scale shifts in seasonal movement patterns between these two time frames were explored. Movement behaviour was analysed at a finer spatial and temporal scale by comparing the rate of movement within different areas, during the day and night. A spatially-explicit approach for characterizing movement behaviour within discrete grid squares was used to identify seasonal patterns in the distribution of movement behaviour indicative of stress. After ten years of highly stressful poaching conditions, extensive seasonal migrations to the north and west of Zakouma National Park persist. At a finer spatial scale movement behaviour indicative of human-induced stress has emerged, especially in the areas utilized to the north of the park. Elephant behaviour to the north of Zakouma, particularly in response to the main road intersecting this area, suggests that barriers to dispersal may soon arise. Furthermore, the absence of migration in the wet season of 2013, after the data cut-off point for this study, suggests that the migration behaviour of this elephant population may be changing. In light of these findings, land-use planning in this area should be carried out in order to realign the boundaries of protected areas to include important elephant dispersal areas.

Keywords: telemetry, migration, movement behaviour, anthropogenic influence, connectivity

1. Introduction

Variability within ecosystems across time and space has long been acknowledged by ecologists, but was poorly integrated into early theoretical frameworks (Wu & Loucks 1995, Clark 2010). The recent development of technology enabling the explicit incorporation of spatial and temporal heterogeneity into explanations of population dynamics and processes has triggered a paradigm shift in ecology (Wu & Loucks 2005). Today remotely sensed data, geographic information systems and computing have become accessible to a wide range of users, increasing the degree to which the dynamic nature of ecosystems can be included in ecological studies (Turner et al. 2003, Clark & Gelfand 2006, Hebblewhite & Haydon 2010, Petorelli et al. 2011). These developments in technology, paired with the adoption of an ecological framework that incorporates heterogeneity and scale (Levin 1992, Wu & Loucks 2005), have resulted in many novel approaches to understanding the processes responsible for animal movement (Morales et al. 2004, Patterson 2008, Benhamou 2011, Holdo & Roach 2013).

1.1. Advances in the study of animal movement

The ability to move is a characteristic common to all eukaryotes, and forms the foundation of many evolutionary and ecological processes (Nathan et al. 2008). Studying the causes and consequences of the movement of individual animals has increased ecologists' insight into animal behaviour and the spatial dynamics of populations (Schick et al. 2008, Owen-Smith, Fryxell & Merrill 2010, Cumming et al. 2012). The emergent paradigm of movement ecology asserts that four key components are required to disentangle the mechanisms driving movements at various scales: internal state, motion ability, navigation ability and external conditions (Nathan et al. 2008). Movement pattern thus results from interactions and trade-offs between the physiological state of an organism and the external conditions to which it is exposed (Fryxell et al. 2008, Nathan et al. 2008). Motion ability essentially determines the range within which an organism is capable of moving and navigational ability affects the timing and repeatability of movements, and is dependent on the cognitive mapping ability of an organism (Lima & Zollner 1996, Fryxell et al. 2008). Due to the imminent threat of habitat loss and climate change and the resultant shifts in the spatial distribution and accessibility of resources, a particular focus in the

field of movement ecology has been placed on the interaction between individuals and their environment (Schick et al. 2008).

In order to maintain fitness, large mammalian herbivores must respond to spatial patterns and variability in the distribution of resources through time and space (Fryxell & Sinclair 1988, Bailey et al. 1996). Movement is a key feature allowing herbivores to achieve this and survive in seasonally variable, patchy landscapes (Mysterud et al. 2001, Wang et al. 2006). Migrations or extended movements require the expenditure of energy and can result in exposure to harmful elements (Senft et al. 1987). A trade-off thus exists between large scale movements between resource patches and remaining resident in a given area (Charnov 1976, Senft et al. 1987, Fryxell & Sinclair 1988, Owen-Smith et al. 2010). Certain abiotic factors, such as the availability of water and seasonal weather patterns further contribute to mega-herbivore spatio-temporal organisation (Bailey & Provenza 2008). Habitat selection is commonly studied on a much larger spatial and temporal scale than studies of foraging behaviour and the social drivers of animal movement (Schick et al. 2008, Owen-Smith et al. 2010, Cumming et al. 2012).

Following the framework of landscape ecology Kotliar and Wiens (1990) proposed a hierarchy of patch structures in order to provide a spatial and temporal scale of foraging behaviour. The smallest unit at which organisms respond to environmental heterogeneity was defined as a grain (Kotliar & Wiens 1990). Moving up the hierarchy, grains were aggregated at successively higher levels to form distinguishable patches of foraging behaviour in time and space (Kotliar & Wiens 1990, Bailey et al. 1996). For large mammalian herbivores the grain is defined as a bite lasting only a few seconds and aggregates of this and other behaviours extend up the hierarchy to the extent of a lifetime range (Bailey et al. 1996, Owen-Smith et al. 2010). A foraging area is defined as a habitat patch in which an animal exhibits behaviour of feeding, walking or standing alert at a temporal scale of one to four hours, while the daily range comprises 12 to 24 hours of foraging, travelling, drinking, and resting through a suite of habitats (Bailey et al 1996, Owen-Smith et al. 2010). A home-range is the area inhabited by an individual for three to twelve months and comprises of a landscape region within which growth, reproduction and mortality occur (Bailey et al 1996, Owen-Smith et al. 2010). Home-ranges can be seasonally variable in areas exposed to contrasting seasonal weather patterns (Owen-Smith et al. 2010).

Telemetry has become an important tool for monitoring the spatial distribution of many wildlife species, and is especially valuable in studies involving species that move through large areas, that may not be accessible to researchers throughout the year (Cagnacci et al. 2010, Hebblewhite & Haydon 2010). The resulting data are however often noisy and come with their own set of challenges during data analysis (Morales et al. 2004, Schick et al. 2008, Hebblewhite & Haydon 2010). One of the biggest challenges in analysing telemetry data is the mismatch in scale between movement data and the conditions to which the animal was exposed, as well as its behavioural state, within discrete time frames (Frair et al. 2010). Much work has focused on the location of intensively utilized areas within an animal's home-range as these can provide information on the key habitat features driving herbivore distribution, as well as the behavioural mechanisms used by herbivores to locate favourable areas within the landscape (Barraquand & Benhamou 2008). Correlated random walks have been widely used to carry out theoretical studies of movement ecology based on the assumption that animal movements switch between discrete movement modes resulting from trade-offs between internal and external state (Bartumeus et al. 2005, Morales et al. 2005, Nathan et al. 2008, Holdo & Roach 2013). These theoretical developments have resulted in the general acceptance that animals exhibit facultative switches between defined movement modes depending on the conditions to which they are exposed at a given time (Fryxell et al. 2008, Nathan et al. 2008).

The successive-step nature of telemetry data results in spatial and temporal autocorrelation of successive movements, where movements near to each other in space and time are generally more similar than those further apart (Legendre 1993, Elith & Leathwick 2009). The autocorrelation of spatial data violates the assumption of independence required for many statistical tests, highlighting the importance of the incorporation of the spatial distribution and temporal scale of telemetry data into ecological models (Legendre 1993, Patterson et al. 2008). State-space models provide an analytical tool that is capable of accounting for autocorrelation of spatio-temporal data, and incorporating many of the important emergent factors that drive movements: ecological, physiological and environmental (Patterson et al. 2008). Spatial autocorrelation additionally provides a useful tool for exploring the patchy nature of the distribution of different movement behaviours (Legendre 1993, Wittemyer et al. 2008).

Although the methodological framework of movement ecology has greatly advanced in the last few decades there is still room for refinement (Schick et al. 2008, Postlethwaite, Brown & Dennis 2013). Many methods for the analysis of movement data are computationally difficult and require extensive statistical knowledge to avoid erroneous interpretations (Bolker et al. 2008, Postlethwaite, Brown & Dennis 2013). For example methods using random walks involve Markov models and Bayesian fitting techniques, limiting these methods to a group of users with advanced statistical and programming knowledge (Clark & Gelfand 2006, Postlethwaite et al. 2013). A balance must be struck between complex information on the fine scale movement behaviour of individuals within a population, versus population level patterns (Hebblewhite & Haydon 2010, Postlethwaite et al. 2013). Approaches that have garnered attention in encapsulating a trade-off in this regard are spatially-explicit methods of empirically categorizing movement behaviour (Wall et al. 2013) as well as the use of spatial autocorrelation as a tool for investigating the patchy nature of movement behaviour (Legendre 1993, Wittemyer et al. 2008, Elith & Leathwick 2009).

1.2. The status of elephants and their natural movement patterns in Africa

Habitat fragmentation has become one of the most imminent threats to biodiversity, largely due to the disruption of the dispersal of organisms (MacArthur & Wilson 1967, Sanderson et al. 2002). In the face of rapid human population increase, and the expansion of anthropocentric landscapes transformed to support the demands of human consumption, wildlife areas are coming under increasing pressure (Myers et al. 2000, Sanderson et al. 2002). Furthermore, the heterogeneous nature of ecosystems is continuously becoming more pronounced, often in novel ways and at a much greater rate than natural fluxes (Kareiva & Wennergren 1995). Many wildlife areas in Africa are not fenced and as such the land surrounding gazetted protected areas is important for the persistence of dispersal by species that require large areas to satisfy their resource requirements (Graham et al. 2009). Fencing of protected areas can bring about benefits through the reduction of human-wildlife conflict and the exclusion of wildlife from human dominated landscapes (Boone & Hobbs 2004). Conversely fences truncate migration routes, confining animals that naturally disperse over large areas (Boone & Hobbs 2004, van Aarde & Jackson et al. 2007, Gadd 2012). This can result in a suite of adverse effects including habitat destruction by herbivores that become too abundant and are unable to move away from over used

areas (Cumming et al. 1997, Whyte, van Aarde & Pimm 1998) or large scale die offs of herbivores cut off from important resources (Mbaiwa & Mbaiwa 2006).

Wildlife faces a higher risk of persecution in the human-occupied landscapes outside of protected areas, and the preservation of wildlife within these areas is generally uncertain (Myers et al. 2000, de Boer et al. 2013). Furthermore, there is often a prevalence of human-wildlife conflict in these zones, resulting in an antagonistic relationship between humans and wildlife which further threatens the persistence of wildlife movements outside of protected areas (Hoare & Du Toit 1999). The maintenance of corridors of natural habitat through human-dominated landscapes is expected to promote and maintain flow between isolated habitat fragments (Beier & Noss 1998, Haddad et al. 2003). Corridors have become an important, yet controversial, method of maintaining biodiversity, preventing population extinctions, reducing inbreeding and allowing natural levels of association between populations (Hobbs 1992, Simberloff et al. 1992, Beier & Noss 1998). The contention surrounding the efficacy of corridors as a conservation tool hinges on the argument that although corridors may mitigate the effects of habitat fragmentation, they will most likely not be capable of compensating for the overall loss of habitat currently taking place (Hobbs 1992, Simberloff et al. 1992, Beier & Noss 1998, Harrison & Bruna 1999).

In the few areas where African elephants can continue to make use of their historic migration routes it is clear that seasonal movements between different feeding grounds exhibit a fundamental element of their life history (Galanti et al. 2000, Wittemyer et al. 2008, Lindsay 2011). As the largest terrestrial herbivore, the elephant is a dietary generalist in order to account for its sizeable resource requirements and the seasonal, and often low-quality, vegetation available in semi-arid environments (Lindsay 2011). Elephants must however still make extensive foraging movements in order to satisfy these large absolute metabolic needs (Wittemyer et al. 2008, Graham et al. 2009, Lindsay 2011). Seasonal migrations and the maintenance of corridors linking isolated feeding grounds are thus of particular importance in the case of the African elephant, since the habitat of this species has become severely fragmented (Galanti et al. 2000, Douglas-Hamilton et al. 2005, Blake et al. 2008).

The African elephant is listed as vulnerable; however this status varies extensively through the distribution of this species in Africa (Blanc et al. 2007). In southern Africa elephant populations have often become too large for the areas they are restricted to, resulting in habitat degradation

and a decrease in biodiversity due to elephant environmental engineering altering or eliminating the habitat of small mammals, invertebrates and birds (Cumming et al. 1997, Whyte et al. 1997). In contrast to this elephant numbers are decreasing rapidly elsewhere in Africa, primarily due to high levels of poaching and a lack of effective conservation practices (Bouché et al. 2011). As a result a number of elephant populations, especially in west and central Africa, have been reduced to a critically small size, placing elephants at risk of becoming locally extinct in these regions (Barnes 1999, Bouché et al. 2011). This highlights the importance of enforcing effective conservation programmes in these areas. The conservation priority of these elephant populations is reinforced by the suggestion that the savannah elephants of West Africa may have diverged from those in southern and east Africa at a level high enough to merit further investigation into the genetics of these two populations (Bouché et al. 2011). Elephants are primarily poached for their ivory, which is an easily accessible, valuable commodity, in high demand, and as such is exploited in the third world countries that make up the African elephant's range (Bouché et al. 2011). Furthermore poaching is related to socio-economic and political stochasticity, with instability in this regard seeing concomitant increases in poaching (Barnes 1999, Smith et al. 2003). Since independence west and central Africa have been particularly politically unstable regions (Barnes 1999). Furthermore, elephants are highly social, long lived animals and thus poaching not only depletes their numbers but can cause long term disruptions of the social structure and physiological state of a population (Gobush et al. 2008, Jachowski et al. 2013a).

1.3. Elephant movement behaviour

The spatio-temporal movement behaviour of African elephants, as well as their distribution, is shaped by several interacting factors (Harris et al. 2008, de Boer et al. 2013). Elephants carry out optimal foraging, through the avoidance of exposure to unnecessary risks or energy expenditure, where possible, when moving through the landscape to locate resources (Charnov 1976, Harris et al. 2008). As a result elephants spend disproportionately more time in certain core areas within their home ranges, where resource conditions are favourable (Dolmia 2004, van Aarde et al. 1999, Wall et al. 2013). These core areas often vary seasonally, particularly in areas with a high degree of climatic variation across seasons (Dolmia 2004, Galanti et al. 2005, Leggett 2006, Ngene et al. 2009, Wall et al. 2013). The organisation of elephants into discrete home-ranges is a result of selection for, and preferred utilization of, areas that contain favourable resources, but

social interaction and intra-specific competition also affect these choices (Galanti et al 2005, Wittemyer et al. 2008). Elephants are highly social animals with complex, multi-tiered social structures (Archie, Moss & Alberts 2006, Wittemyer et al. 2005). Associations between different tiers in the social system occur in a fission-fusion manner determined by the social and ecological costs and benefits to which a society is exposed at a given time (Western & Lindsay 1984, Wittemyer et al 2005). The position of an individual in this social hierarchy can have an effect on its internal state through intra-specific competition or reproductive drive (Wittemyer et al. 2008). Furthermore, the ecological conditions to which an elephant population is exposed have been found to affect social unit size, with social cohesion and group sizes decreasing during the dry season, in semi-arid ecosystems, and aggregations forming in response to high predation pressure (Wittemyer et al. 2005).

Rate of displacement can be used to infer activity states or contrasting movement behaviours at different temporal scales and in different areas (Owen-Smith et al. 2010). Elephant movements within core areas are observed to be slower and more tortuous than relocations between core areas or foraging areas, which generally take place in a more rapid and directed manner (Galanti et al. 2000, Douglas-Hamilton et al. 2005, Graham et al 2009, Wall et al. 2013). Furthermore, during the dry season, when resources are patchily distributed, displacement rates are generally higher than those observed during the wet season (Ngene et al. 2009, Leggett 2009). Elephants are active both during the day and at night, although they are observed to be relatively inactive during the heat of the day (Leggett 2009). In semi-arid areas, where high daytime temperatures are reached, increased activity during the cooler temperatures experienced at night is observed, paired with periods of rest at midday and for much of the night, resulting in daily cycles of movement (Leggett 2009).

There is large variability in the extent of the areas within which different populations of African elephants range, with some populations carrying out extensive seasonal migrations (Leggett 2009, Wall et al 2013), and others remaining sedentary (Galanti et al. 2005). Water plays an important role in determining the spatio-temporal distribution of elephants, a water dependant species (Western & Lindsay 1984, Dunkin et al. 2013), especially in semi-arid, seasonally variable ecosystems (de Beer & Van Aarde 2008, Harris et al. 2008, Wall et al. 2013). During the wet season the replenishment of ephemeral water sources allows elephants more freedom of

movement (Galanti et al. 2005). Within discrete ecosystems the distribution and quality of food and water is an important determinant of the spatio-temporal organisation of elephants, however at a continent wide scale anthropogenic influence and the economic status of the areas on the peripheries of protected areas seem to play a more important role in determining elephant densities (de Boer et al. 2013).

At certain times of the year, important resources can be located outside of protected areas, often resulting in elephant movements into human occupied landscapes in unfenced systems (Douglas-Hamilton et al. 2005, Galanti et al. 2006, Graham et al. 2009). In areas utilized outside of protected areas elephants have been found to adapt their behaviour, when exposed to real or perceived danger, in order to reduce human encounters (Douglas-Hamilton et al. 2005, Galanti et al 2005, Graham et al. 2009, Kangwana 2011, Granados, Weladji & Loomis 2012, Jachowski et al. 2012). Elephants generally avoid human settlements, and if areas near settlements are utilized these visitations occur at night (Galanti et al. 2006, Granados et al. 2012, Graham et al. 2009, Kangwana 2011). Conversely in some areas elephants actively seek out the cultivated land on the outskirts of settlements in 'crop-raiding' activities, which can bring about damage and loss of property to communities and result in human-elephant conflict (Hoare & Du Toit 1999). Douglas-Hamilton et al. (2005) found that in an unfenced mosaic of protected areas and areas utilized by elephants outside of protected areas, swift elephant movements were made through corridors bridging human occupied landscapes, a behaviour termed 'streaking'. Elephants exposed to a high degree of human induced stress have been found to carry out 'streaking' behaviour when relocating in human-occupied landscapes, and are observed to seek refuge in pockets of dense vegetation, within which movement is restricted (Ruggiero 1990, Douglas-Hamilton et al. 2005, Galanti et al. 2006, Jachowski et al. 2012, Jachowski, Slotow & Millspaugh 2013b).

1.4. The Zakouma National Park elephant population

Few elephant populations remain in west and central Africa, the majority of which are spatially isolated and have been reduced to small population sizes by high levels of poaching (Blanc et al. 2007). The Zakouma National Park elephant population is one such example. During the wet season there is an extensive movement of wildlife, including the elephant population, out of the park's boundaries into the areas to the north and west of the park. The area utilized by this

elephant population is thus effectively over three times the size of the National Park or about 11 000 km^2. The sheer size of the area in which this elephant population must be conserved, as well as an extended period of political instability in Chad have allowed unrestricted poaching of this population. A number of aerial censuses have been carried out in Zakouma National Park and have collectively shown a dramatic decrease in elephant numbers from an estimated 4351 animals in 2002 to 430 in 2013 (Mackie 2004, Fay et al. 2006, Potgieter et al. 2011). The management of Zakouma National Park was taken over by African Parks (https://www.african-parks.org/) at the end of 2010 and under African Parks management anti-poaching efforts have been improved. At low poaching levels and favourable social and environmental conditions, elephants have the potential for rapid population growth and recovery from small population sizes (Foley and Faust 2010). The improvement of anti-poaching measures has reduced poaching substantially and as a result the Zakouma National Park elephant population may be at a turning point, moving towards population recovery.

Three Zakouma National Park elephants were fitted with GPS collars in 2000 and another five in 2002 and were studied by Dolmia (2004). Dolmia's findings gave a clear insight into the movement patterns and behaviour of the Zakouma National Park elephant population, as well as information on their home-ranges and breeding behaviour (Dolmia 2004). The population at the time of his study was however well over 4000 elephants (Mackie 2004) and the population was split into two groups with little home-range overlap between the group of elephants predominantly found in the south-eastern section of the park during the dry season, and those found in the north-eastern section of the park at this time (Dolmia 2004). Furthermore the north-eastern group of collared animals were found to migrate to the north of the park during the wet season, while the south-eastern group of collared animals migrated either to the west or south-west of the park (Dolmia 2004).

1.5. Rationale, objectives and hypotheses

Although the Zakouma National Park elephant population has become stable in the past few years, increasing political instability and unpredictability in the countries neighbouring this region is expected to bring about increased poaching (Bouché et al. 2011). The importance of the information gained from this study is therefore twofold: firstly the reduction in the size of this

elephant population demands information on the movement patterns and behaviour of the Zakouma elephants in order to build up a database of information on the ranging patterns of an isolated, vulnerable elephant population. Secondly, if this elephant population is at a turning point and is heading towards population recovery, the identification of areas of high conservation concern, especially outside of the national park, are likely to be essential for conservation planning. The high impact of confined elephant populations on woodland habitats in southern Africa highlights the importance of the maintenance of elephant migration routes and corridors for expanding populations, and necessitates studies on elephant populations that still exhibit natural migrations. In addition to this, information about the current state of ecosystems and the behaviour of keystone species can act as an important baseline to monitor changes in ecosystem functioning in the future, and in the face of global change.

As previously outlined, recent frameworks for the study of movement ecology suggest that it is important to define the *where, when, how* and *why* of large scale animal migrations (Nathan et al. 2008). In line with this I focused my analyses on addressing some of these questions for the migration of the Zakouma National Park elephants through a seasonally variable ecosystem. Firstly, I assessed how movement patterns have changed after an extensive period of poaching and a ninety percent decrease in the size of the Zakouma National Park elephant population. I compared coarse spatial and temporal scale movement patterns from a period when the elephant population was on the threshold of reaching damagingly high densities (Calenge et al. 2002), to those exhibited by the current, and dramatically reduced population. In addition to this I explored the *how*, *where* and *when* aspects of the population's movements between 2011 and 2013 in more detail. Using Global Positioning System data from thirteen elephants between 2011 and 2013 in combination with data on annual rainfall over the study period I compared the timing of movements away from the National Park, as well as the timing of the return from the wet season home-ranges, across years and the relationship between these timings and rainfall. Movement speed, used as a proxy of movement behaviour, was compared between different areas and time frames to identify patterns in movement behaviour within this ecosystem. More explicitly the hypotheses examined were that (i) movement speeds outside of Zakouma National Park are expected to be higher than those within the protected area, (ii) nocturnal movement speeds are expected to be higher than diurnal movement speeds in areas utilized outside of the park where there is more exposure of elephants to people, and (iii) a seasonal effect on nocturnal and diurnal

movement speeds is expected in response to average upper temperature and resource availability. The seasonal distributions of low and high movement speeds and turning angles in spatially explicit grid squares was used to illustrate the spatial organisation of different movement behaviours imposed by the variable conditions during the contrasting seasons, and different areas used during these times. At a fine spatio-temporal scale elephants are expected to move more quickly through areas where they perceive danger and where resource conditions are poor, while slower movements are expected under favourable resource conditions and little disturbance. Contrasting movement behaviours are additionally expected to be distributed in a patchy manner.

2. Methods

2.1. Study area

2.1.1. The greater Zakouma ecosystem

Zakouma National Park (11°N 20°E), in south-eastern Chad, covers an area of 3054 km² (Fig. 2.1) and is one of the last big game strongholds in north-central Africa (Brugière & Scholte 2013). Zakouma was initially established as a faunal reserve in 1958 following declines in a number of wildlife species in the region, due to excessive hunting (Poilecot, Djimet & Ngui 2010). The protection offered by the faunal reserve allowed wildlife numbers to recover and increase, which in turn resulted in an increase in the number of poachers exploiting the now abundant wildlife (Poilecot et al. 2010). This prompted the Chadian government to declare the area a national park in 1963 resulting in the recovery of populations of most wildlife species (Mackie 2004, Brugière & Scholte 2013). In contrast to the norm in southern Africa, the park is not fenced resulting in free influx and efflux of wildlife, and additionally making boundaries more porous to illegal entry by people (Boone & Hobbs 2004). The park is however completely surrounded by the Bahr Salamat Faunal Reserve, (20 000 km^2) which although inhabited by people forms an important buffer area around the National Park (Brugière & Scholte 2013). Although the park's elephant population is found within the park boundaries for the majority of the year, areas to the north and west of the park are utilized during the wet season (Mackie 2004, Fay et al. 2006, Potgieter et al. 2011). With the inclusion of these seasonal home-ranges outside of Zakouma National Park, the area utilized by the Zakouma elephants is about 11 000 km^2.

2.1.2. Seasonal weather patterns, vegetation, topography and hydrology

Zakouma National Park lies in the East Sudanian savanna ecoregion within the Sudano-sahelian climate zone (Burgess et al. 2004, Brugière & Scholte 2013). The rainfall pattern is unimodal, beginning in late May to early June and ending in October. An annual average of 750 mm of rainfall is experienced, with rainfall almost exclusively limited to the months of the wet season (Calenge et al. 2002, Dolmia et al. 2007). The onset of the rains and the amount of precipitation is however very variable between years (Calenge et al. 2002). A cool dry season follows the wet

season from November to January, followed by a hot dry season from February to May with temperatures regularly reaching 45 degrees Celsius (Dolmia et al. 2007). The western and eastern sections of the park are differentiated by topography, hydrology, and drainage density, while the park's vegetation is patchily distributed (Fig. 2.2).

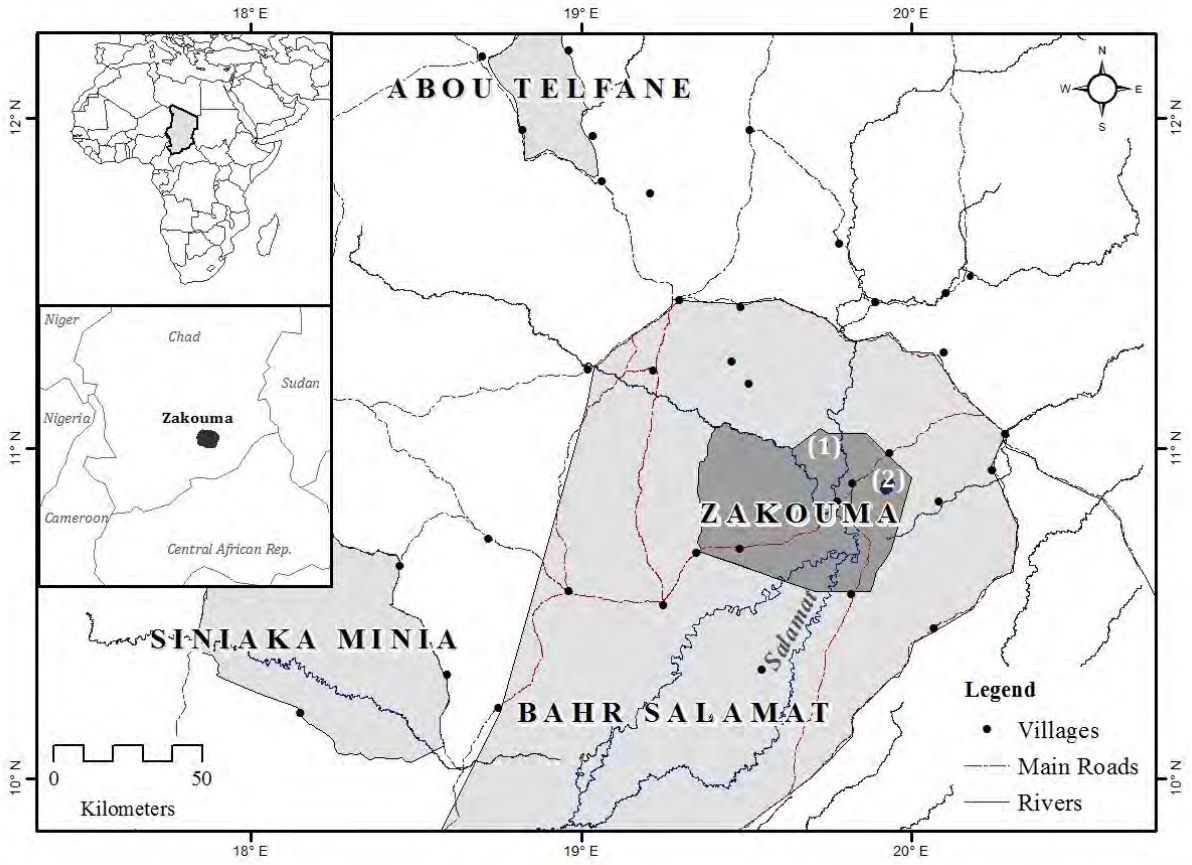

Fig. 2.1. *Map of the greater Zakouma ecosystem showing the location of major roads and rivers, and the key human settlements in the region. Zakouma National Park is represented by the dark grey area, while Faunal Reserves are symbolised by light grey areas. The important dry season water bodies, (1) Tororo and (2) Rigueik Swamp, are labelled, as well as the Salamat River. Inset maps show the location of Chad in Africa as well as the location of Zakouma National Park within Chad.*

The vegetation in the north and east of the park is dominated by *Acacia seyal* savanna, while the centre and south-west of the park is mostly made up of Combretaceae and Caesalpiniaceae savanna (Calenge et al. 2002, Fig. 2.2). There are a number of large wetlands and grass plains in the eastern half of the park, which provide important grazing at certain times of the year (Calenge et al. 2002, Fig. 2.2). The landscape is relatively flat, with the exception of a few

inselbergs to the north and south-west of the park and one in the south of the park. There is additionally a slight decrease in elevation from west to east. The substrate in the eastern half of the park and extending north are Solonchaks and Pellic Vertisols (black cotton soil) while the western half of the park, and the areas to the west of the park, are dominated by Ferric Luvisols (Land and Water Development Division, FAO 2003). The surface water of the park is centred in the eastern half of the park as a result of lower elevation, high drainage density and soil type (Poilecot et al. 2010). Several large drainage systems to the north and the north west of the park terminate in the eastern half of Zakouma National Park and on the Garra plains to the east of the park. The Garra plains cover the area adjacent to the park on its eastern border and become inundated during the wet season months. The high rainfall during the wet season additionally floods large areas, predominantly in the lower elevation eastern half of the park (Dolmia et al. 2007). During this time there is an extensive movement of wildlife, including the elephants, away from the eastern section of Zakouma National Park, and often beyond the park's boundaries into areas to the north and west of the park.

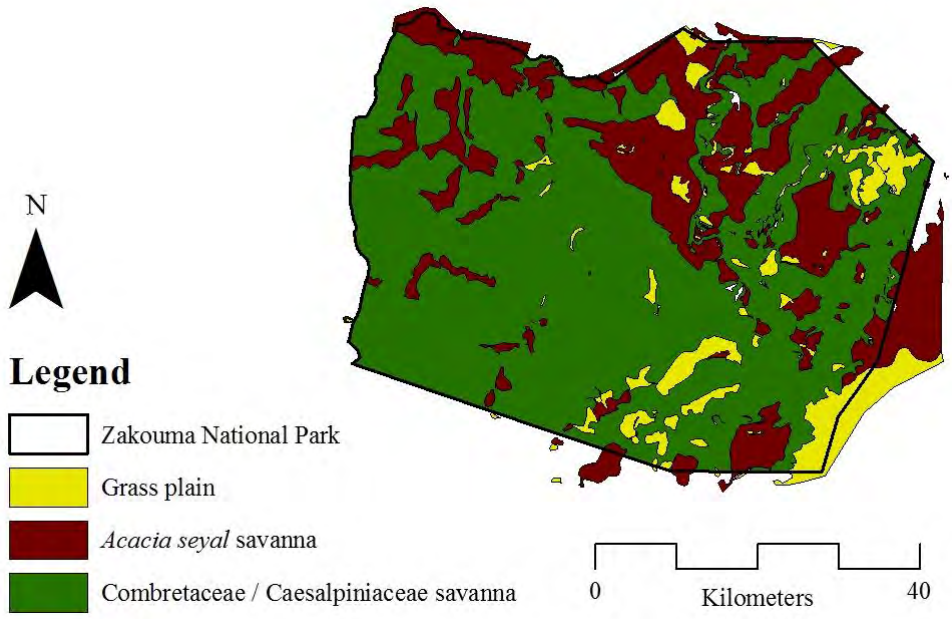

Fig. 2.2. *Map showing the dominant vegetation types in Zakouma National Park, Chad. Map adapted from Poilecot, Saidi & Bémadjin Ngakoutou (2004).*

Seventy percent of the water bodies in Zakouma National Park dry up by the end of the dry season with only the Tororo water body, Rigueik swamp, and the large pools along the Salamat River (Fig 2.1) which are all located in the eastern half of the park, retaining water until the start of the rains (Dolmia 2004). Very few water bodies hold water throughout the dry season in the area to the west of Zakouma National Park while several large water bodies persist throughout the year to the north of the park. The water sources outside of the park's boundaries are however heavily utilized by both sedentary and nomadic people and their livestock during the dry season months.

2.2.3. Human influence

The human population inhabiting the areas surrounding Zakouma National Park is comprised of nomadic pastoralists and small scale agriculturists. The nomadic tribes carry out a transhumance migration moving northwards to the southern fringe of the Sahel at the onset of the rains, in order to avoid flooding, and the associated increase in livestock and human diseases (Sheik-Mohamed & Velema 1999), in their dry season homesteads and to exploit pulses in vegetation growth to the north (Breman & de Wit 1983). These movements take place around the national park, with the northward leg of their journey occurring at a similar time, and through a similar area, as that of the elephant population. Once water and forage resources become depleted in the areas utilized by the transhumance population during the wet season, a southward movement commences. This brings the influx of about 50 000 nomadic people into the areas on the periphery of Zakouma National Park, with population density highest to the east and south of the park (M. Antonínová pers. comm. January 2014). The dominant crop cultivated in the region is sorghum (*Sorghum bicolor*) which is planted at the end of the rainy season, as the flood plains begin to dry out (Dolmia 2004). The soil, usually black cotton soil, generally retains enough water to carry the crops through to harvest in February, four months into the dry season. The village of Bone Daoud is situated within the park boundaries, due to the religious associations of this tribe to the Bone batholith. Situated in the drier, south-western section of the park this village is limited by the provision of water from a single well, and there are restrictions on the amount of cultivation and expansion allowed on the periphery of the village.

Chad is classified as a least developed country and is one of 12 countries expected to maintain fertility rates above 3.5 up to 2050, which is predicted to result in the population tripling in the next 50 years (UNDESA 2013). Although human fertility is high in the areas surrounding Zakouma National Park recurrent political instability has hindered the development of civil society and the provision of basic services for the population (UNDESA 2013, Brugière & Scholte 2013). As a result of this, and a harsh and unpredictable way of life in a stochastic political and environmental climate, life expectancy in Chad is one of the lowest in Africa, and infant and child mortality is high (UNDEP 2013). Health care is poor in these areas and is especially low for the transhumance people of the region (Sheik-Mohamed & Velema 1999). In summary the human population surrounding Zakouma National Park is characterized by high fertility, poor education and low employment and income. The region is furthermore bordered by countries currently experiencing civil strife, and although Chad is politically stable at present, this status is unpredictable. These are factors that have influenced, and may continue to influence, the population dynamics and movements of the Zakouma elephants.

2.2. Elephant location data

Ten elephants were fitted with Global Positioning Satellite (GPS) collars in April 2011 and another six in April 2012. The telemetry data employed in this study were collected by African Parks and the Chadian Ministry of Environment and Fishery Resources in Zakouma National Park. The GPS collars were manufactured by African Wildlife Tracking (http://www.awt.co.za/), and the collars, in combination with the lead counter weight used to ensure the transmitter is maintained dorsally, weigh a total of 13 kilograms (S. Haupt pers. comm. 2013). The satellite transmitter in these collars transmits to a geostationary Inmarsat satellite in near real time (S. Haupt pers. comm. 2013). The precision of the collars is nine metres for 3D readings and 90 metres for 2D readings i.e. the "true" location of the animal is within a nine metre radius of the GPS collar location fix for 3D readings and a 90 metre radius for 2D readings (S. Haupt pers. comm. 2013). Elephants were immobilised using standard procedures, darting was done on foot and it was ensured that minimal stress was caused to the animals. A total of seven males and nine females were fitted with GPS collars between the two collaring operations. Adult female elephants occur in cohesive family groups and thus movements captured by satellite collars deployed on female elephants are representative of the movements of an entire family group

(Wittemyer et al. 2005, Moss & Lee 2011). At the onset of the wet season, when the majority of the elephant population make seasonal movements outside of the park boundaries (Potgieter et al. 2011), two general movement patterns arise: a westward and a northward migration route. Both routes were represented by a similar sample size of collared elephants (Table 2.1).

Table 2.1. *General information for the 2011-13 study animals outlining the duration of tracking, the direction of movement outside of the National Park during the wet season; the total distance travelled during the study period (May 1, 2011 to April 30, 2013); the percentage of the study period spent within Zakouma National Park's boundaries; and the maximum distance from the park boundary during the study period.*

Elephant ID	Sex	Age (years)	Wet season movement	Total Distance (km)	Time inside National Park	Max. distance from park boundary (km)	Global success rates (% deleted fixes)
Full study period (May 1, 2011 to April 30, 2013):							
Z1	M	15-19	Resident	8126	80%	15.5	7.39%
Z4	M	17-19	West	9322	86%	67.5	9.69%
Z7	M	19	West	9996	85%	122.5	12.86%
Z8	M	15	West	9457	84%	66.4	8.78%
Z2	F	13-15	North	7727*	89%	98.2	6.73%
Z3	F	10-11	West	8921	83%	66.6	9.97%
Z10	F	10-14	North	9612	80%	98.7	8.05%
Half study period (May 1, 2011 to April 30, 2012):							
Z6	F	19	North	5034	76%	98.0	6.48%
Half study period (May 1, 2012 to April 30, 2013):							
Z5A	M	10-15	North	3958	63%	124.7	8.90%
Z12	M	18	Resident	3027	81%	11.3	8.64%
Z13	M	16	North	4422	78%	50.4	10.61%
Z11	F	18	West	4734	89%	52.5	8.52%
Z15	F	15-20	West	3816	86%	64.0	10.81%

* Data for July and August 2011 missing due to collar malfunction

Male elephants generally separate from their natal herd as sub-adults, after which they adopt complex association patterns including solitary occurrences as well as being found in bachelor herds or family groups (Lee et al. 2011). The GPS tracking results for male elephants are therefore generally taken to be representative for a single animal alone. Although a female bias is favoured in studies of elephant movements following this logic (Graham et al. 2009) the

limitations of darting on foot resulted in a more equal sex ratio. The data for two females collared in 2011 were excluded from analyses as one was poached two months after collar deployment and one collar did not function properly. In addition to this, one female collared in 2012 belongs to a group of five elephants inhabiting an area to the north of the National Park that do not carry out extensive seasonal migrations and are not included in census data. Data for this animal were excluded as this northern population is expected to behave differently to elephants frequenting Zakouma National Park for the majority of the year and the sample size of only a single animal from this population was too small to make comparisons between populations.

GPS location data collected from the 13 study animals were examined for erroneous fixes and duplicates which were removed. This was done manually and through the use of a filter based on the biologically probable speed threshold of 7 km/h (Wall et al 2013). The primary reason for fitting a number of elephants with satellite collars in Zakouma National Park was to better understand the timing and spatial distribution of the seasonal movements of this population as well as to aid monitoring and conservation of the population (Labuschagne 2011). As a result the inter-fix time intervals varied considerably with time (Appendix 1). Data from eight elephants, fitted with Argos collars, between 2000 and 2003 were used for study aims that address the changes in behaviour of this elephant population before and after the period of heavy poaching (Table 2.2). Due to the advances in satellite telemetry technology since the time of this study, the quality of the 2000-3 data are poor compared to the data obtained from the 2011-13 satellite collars, with location fixes occurring at irregular time intervals and in some cases several days passing without location fixes.

2.3. Movement pattern

I assessed the change in range use over a course temporal scale by comparing wet and dry season ranging patterns between 2000 and 2003, and between 2011 and 2013. Location fixes, separated by season, were mapped for the 2000-03 and 2011-13 datasets. The wet season was classified as the period between the first of June and the 31st of October and the dry season as the remaining months of the year in order to segment the data into wet and dry season location fixes. The relocations of the 2011-13 study animals were mapped in combination with up to date location data for human settlements, and the extent of cultivated land in the areas surrounding the park. Average UTM Northing and UTM Easting values during ten day periods nested within months

were plotted for male and female northward-migrating, westward-migrating and resident elephants independently to illustrate the general spatial and temporal trends of seasonal movements for each sex within these three groups in the population. This was carried out for the current data set and for the data collected ten years prior, however only northward-migrating males and females and westward-migrating females were monitored between 2000 and 2003.

Table 2.2. *General information for study animals collared by Dolmia between 2000 and 2003 outlining the duration of tracking, sex, location of collaring, and age when available.*

ID	Sex	Age (years)	Collaring date	Tracking duration	Section of park	Collaring co-ordinates (UTM)	
						Latitude:	Longitude:
M30086A	M	-	10/05/2000	10/05/2000-14/10/2000	North-east	387321	1203566
F30087A	F	35-49	11/05/2000	11/05/2000-13/10/2000	North-east	370469	1198761
F30088	F	35-49	14/05/2000	14/05/2000-10/06/2002	North-east	366748	1197891
M30086B	M	-	01/02/2002	01/02/2002-29/06/2003	North-east	369705	1196327
F30087B	F	-	02/02/2002	02/02/2002-30/06/2003	North-east	376923	1199732
F13505	M	-	03/02/2002	03/02/2002-28/11/2002	South-east	358782	1174062
F13506	F	-	05/02/2002	05/02/2002-28/06/2003	South-east	369192	1179744
M13507	F	-	05/02/2002	05/02/2002-22/04/2003	South-east	375335	1184477

The timing of the initiation of, and return from, the northward and westward migrations across years were plotted in combination with monthly rainfall data for each year. The monthly rainfall data used were rainfall gauge data collected by Zakouma National Park management. Observations of the location and movements of the transhumance population of the area, collected through aerial surveillance and monitoring carried out in 2011, were mapped by month, in combination with the locations of the Zakouma National Park elephant population. This was

only carried out for the months of June to September, in order to correspond with the months during which elephant movements to the west and north of Zakouma National Park predominantly take place. Observations of the location of the transhumance population collected by Zakouma National Park management were mapped using heat mapping in ArcMap 10 (Environmental Systems Research Institute [ESRI] 2010), where the density of observations is illustrated using a gradient of dark (indicating high density) to light (indicating lower densities) shading.

2.4. Movement path metrics

The movement paths of the 2011 to 2013 study animals were projected to the Universal Transverse Mercator (UTM) WGS-84 reference system (Zone 34N) in ArcMap 10 (ESRI 2010) and all further analyses of these spatial data were done on the projected dataset. The 'movement path metrics' command in the Geospatial Modelling Environment (Beyer 2012) was used to calculate movement path characteristics (step length (m), turning angle (°), bearing (°)) between consecutive location fixes for each study animal. The absolute values of turning angles were used, and thus turning angles ranged from 0° to 180° allowing for the use of linear statistics for analyses involving turning angle, as opposed to circular statistics (Valeix et al. 2010). Movement speed in kilometres per hour per inter-fix bridging segment was calculated by dividing the step length (distance between subsequent GPS-location fixes) output from the Geospatial Modelling Environment, converted from metres to kilometres, by the corresponding inter-fix time interval. Due to the deletion of erroneous fixes some inter-fix time intervals were double or even triple the length of the three set time intervals. Movement speeds were therefore examined for a relationship between speed and time interval. There was a trend of decreasing movement speed with increasing time interval above a time interval threshold of 8.5 hours. Movement path metrics calculated for bridging segments with an inter-fix time interval greater than 8.5 hours were therefore excluded from all analyses. Study animals were grouped according to migration path as the conditions experienced along different migration routes vary. This resulted in three groups: westward-migrating animals, northward-migrating animals and resident bulls. Inter-fix bridging segments were categorized as diurnal and nocturnal considering a sunrise time of 06h00 and a sunset time of 18h00. Bridging segments were additionally characterized according to

whether they took place within the boundaries of Zakouma National Park, or outside of the park boundaries.

In order to obtain a spatially explicit measure of movement behaviour the greater area utilized by the Zakouma National Park elephant population was rasterized by dividing the area into 25 km^2 grid squares in ArcMap 10 (ESRI 2010). Mean speed and turning angle values were then calculated for each grid square utilized by the study animals during. These calculations were carried out by season in order to account for variation in movement behaviour and the distribution of the elephant population between seasons. For these analyses the wet season was classified as the start of June to the end of October, as the onset of the rains is variable, either occurring at the end of May or the start of June. The remaining months of the year were classified as dry season months. Histograms of mean grid square speeds and turning angles were plotted and the 5th, 25th, 75th and 95th quantiles were calculated for each movement path metric. Grid squares were subsequently classified according to which percentile (5%: $<5^{th}$ quantile, 25%: $>5^{th}$ and $<25^{th}$ quantile, 50%: $>25^{th}$ and $<75^{th}$ quantile, 75%: $>75^{th}$ and $<95^{th}$ quantile, 95%: $>95^{th}$ quantile) the mean movement speed and turning angle fell within. The grid squares utilized during the dry season and those utilized during the wet season were mapped separately with grid squares colour coded according to (a) the mean movement speed, and (b) the mean turning angle for the dry and wet season respectively. During the wet season when extensive movements outside of Zakouma National Park take place, grid squares were subsequently grouped according to location: completely within the park boundary/to the north of the park/to the west of the park. The proportion of each of the categories of movement behaviour observed was calculated within each of these spatial categories and plotted.

2.5. Data analysis

Statistical analyses were carried out using R 3.01 (R Core Team 2013) and the integrated development environment RStudio (RStudio 2013). The movement speed data were explored following the procedures described by Zuur et al. (2010). The data were grouped according to migration behaviour. These groupings account for the difference between the movement behaviour of males and females by analysing the data of the resident bulls separately to movements of satellite collared elephants associated with breeding herds. Splintering of single satellite collared animals from breeding herds is consistently monitored through Geographic

Information Systems and aerial surveillance in an effort to regularly account for the locations of all elephants in the population for anti-poaching purposes (pers. comm. R. Labuschagne November 2014). Of the satellite-collared northward- and westward-migrating bulls, only one animal was observed to make a solitary movement away from the breeding herd during the study period. As a result male and female movement speeds in these groups were not analysed separately. Furthermore grouping the study animals according to their migration behaviour accounts for the difference in the conditions to which the migrating elephants are exposed to, to the north and the west of the park, as well as the lack of an extensive seasonal migration for the resident bulls.

Speed data were right skewed and variances were heteroskedasctic for some comparisons within groups. The number of observations per individual was additionally unbalanced due to variability in inter-fix time intervals and collaring period between study animals. Generalised linear mixed effects models (GLMM) with speed as dependant variable and collared individual as a random effect were run to account for non-independence of data, and variation in the behaviour of individuals (Gillies et al. 2006, Bolker et al 2008, Rhodes et al. 2009). The error distribution of GLMMs additionally accounts for possible biases associated with non-normal data (Bolker et al 2008, Rhodes et al. 2009). Statistical modelling was performed using the "lme4" package in RStudio (Bates et al. 2013). The key predictor variables in the GLMM for each grouping of study animals were (i) the location of the movement at a coarse spatial scale (inside/outside the national park), (ii) the period during which the movement took place (day/night), and (iii) the interaction between location and period. A gamma error structure and an inverse link function were used to account for over dispersion. Wald chi-square tests were used to identify significance of fixed effects (Bolker et al. 2008) and pairwise comparisons were made using a least squared difference (LSD), adjusted using the Tukey method, for interactions found to be significant. Moran's I statistic was calculated to test for spatial autocorrelation of the mean speed and turning angle values of grid squares, by season, using the Analyses of Phylogenetics and Evolution package (Paradis, Claude & Strimmer 2004) in RStudio (RStudio 2013).

3. Results

3.1. Movement pattern

The core area utilized by the Zakouma National Park elephant population between 2011 and 2013 was situated in the eastern half of the park (Fig. 3.1). Seasonal dispersal away from this area extended up to 123 kilometres north and 125 kilometres west of the park boundary (Table 2.1, Fig. 3.1). During the dry season the elephant population remained in close proximity to the eastern half of the park (Fig. 3.1). During the wet season movements into the western half of the park and out of the park to the west and north took place (Fig. 3.1b). Although extensive movements outside of Zakouma National Park were observed in 2000-03 and 2011-13, the elephant population was observed to be situated within the park boundaries for the majority of the 2011-13 study period (Table 2.1). The movement patterns of the 2011-13 population are similar to those observed for this population between 2000 and 2003, when the population size was much larger (Fig. 3.1).

Some changes in movement patterns over time are however clear. Firstly, the elephant population has not been observed to utilize the areas to the south and east of the national park during the dry season for the past three years (Fig. 3.1b). From 2000 to 2003 some elephants were observed to move out of the park along the Salamat River to the south and to Am Lel to the east of the park, during the dry season months (Fig. 3.1a). Secondly, utilization of the area around Fodjo Swamp (in the east of the northern range) was not observed between 2000 and 2003, while this area formed one of the core areas frequented by the northward-migrating elephants in their wet season range between 2011 and 2013 (Fig. 3.1). Movements to the south-west have additionally become less wide-ranging. Between 2000 and 2003 a breeding herd containing two collared animals was observed to range as far south west as Siniaka Minia Faunal Reserve and spend an extended period of time in this area (Fig. 3.1a), while only one collared bull monitored from 2011 to 2013 ranged as far west as Siniaka Minia (Fig. 3.1b). Lastly the wet season movements to the north of the park for the 2000 to 2003 dataset (Fig. 3.1a) took place over a wider area and were less confined than the movements of the 2011 to 2013 dataset (Fig. 3.1c).

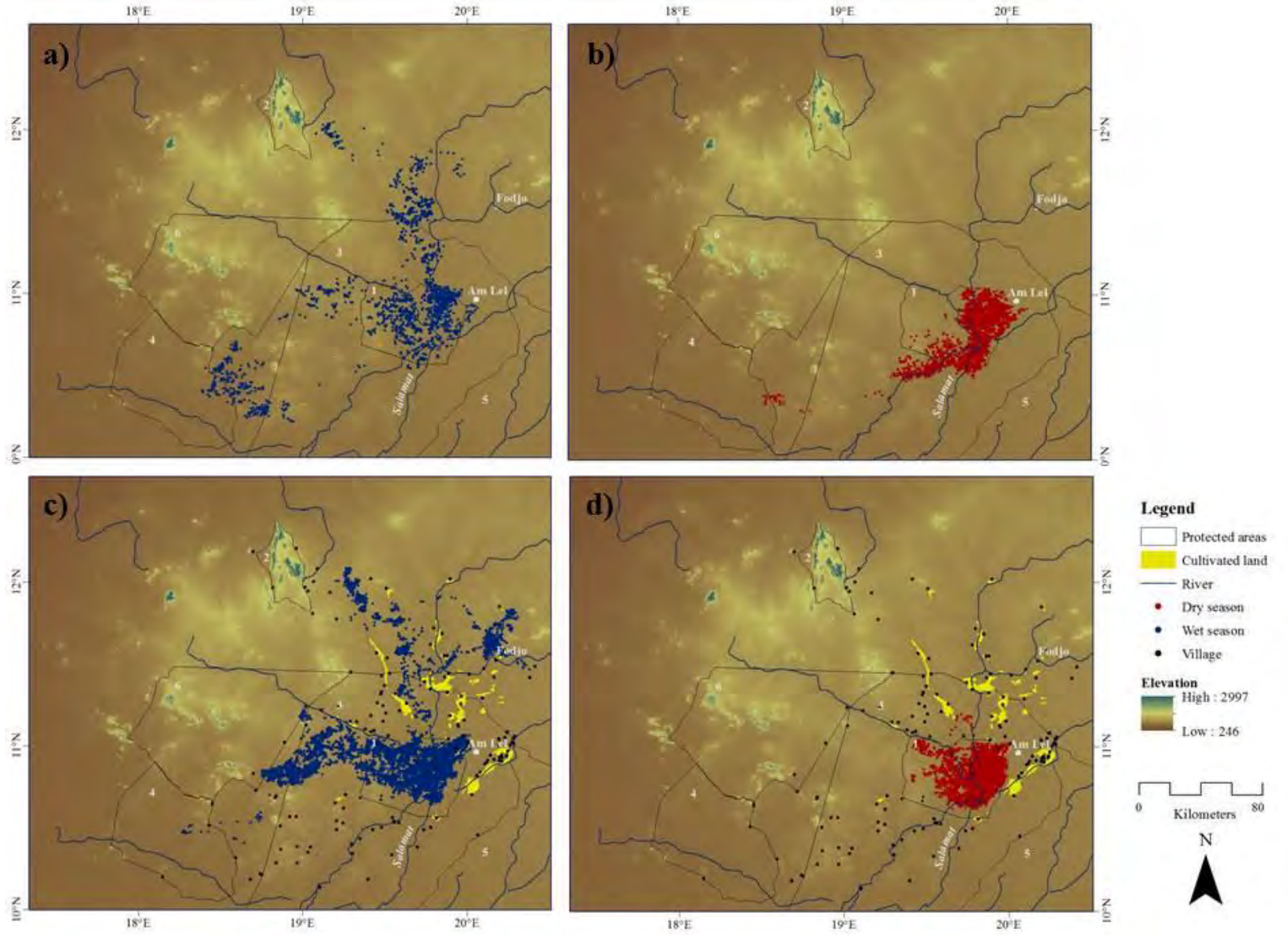

Fig. 3.1. *Maps showing combined GPS positions for a) eight African elephants between 2000 and 2003, and b) thirteen African elephants between May 1, 2011 and April 30, 2013. The more recent map shows the location of villages and cultivated land data collected by African Parks, while accurate data on these attributes is lacking from the earlier study period and is thus excluded. The background image shows elevation and Zakouma National Park is outlined. Select place names are labelled.*

The Zakouma National Park elephant movements have become contracted in the areas utilized to the north of the park (Fig. 3.1b). This is particularly clear for dispersal through the northern corridor which connects Zakouma National Park and the wet season home-range to the north of the park (Fig 3.1b). The area to the north of Zakouma National Park supports a higher density of people than the areas to the west of the park (Fig. 3.1b), and there is a greater degree of agricultural development to the north and east of the park than to the south-west of the park (Fig. 3.1b). The presence of a virtual fence line around Zakouma National Park has become clear, especially in the areas to the south and south-east of the park (Fig 3.1b.). Furthermore, the Zakouma National Park elephant population was not observed to carry out a seasonal migration in the wet season of 2013, after the data cut-off period for this study (pers. comm. L. Labuschagne August 2013). The elephant population did however move away from the core dry season range, in the eastern half of the park, into the western half of the park in the wet season of 2013 (pers. comm. L. Labuschagne August 2013).

Movements away from the core dry season home-range of the Zakouma National Park elephants were observed to take place at the onset of the wet season, between 2011 and 2013 (Fig. 3.2b) and from 2000-03 (Fig. 3.2a). All the study animals from the current tracking duration utilized a similar area within the park during the dry season (Fig. 3.2b), while there was little spatial overlap between the groups of elephants occupying the north-eastern and south-eastern section of the park from 2000-03 (Fig. 3.2a). Resident bulls remained on a relatively constant longitudinal and latitudinal plane throughout the current study period (Fig. 3.2b). The northward migration was initiated at a similar time from 2011-13 and from 2000-03, while westward movements commenced earlier between 2000 and 2003 (Fig. 3.2). Movements out of the park to the wet season home-range of the northward-migrating elephants were observed to take place in a directed manner, while movements to the west were more gradual, with east-west and west-east movements alternating for the first month of the wet season (Fig. 3.2b). In the northern wet season home-range movements between areas utilized for several days were observed, and the return migration from the northern wet season range was more gradual than the dispersal from the park to this area, at the onset of the wet season.

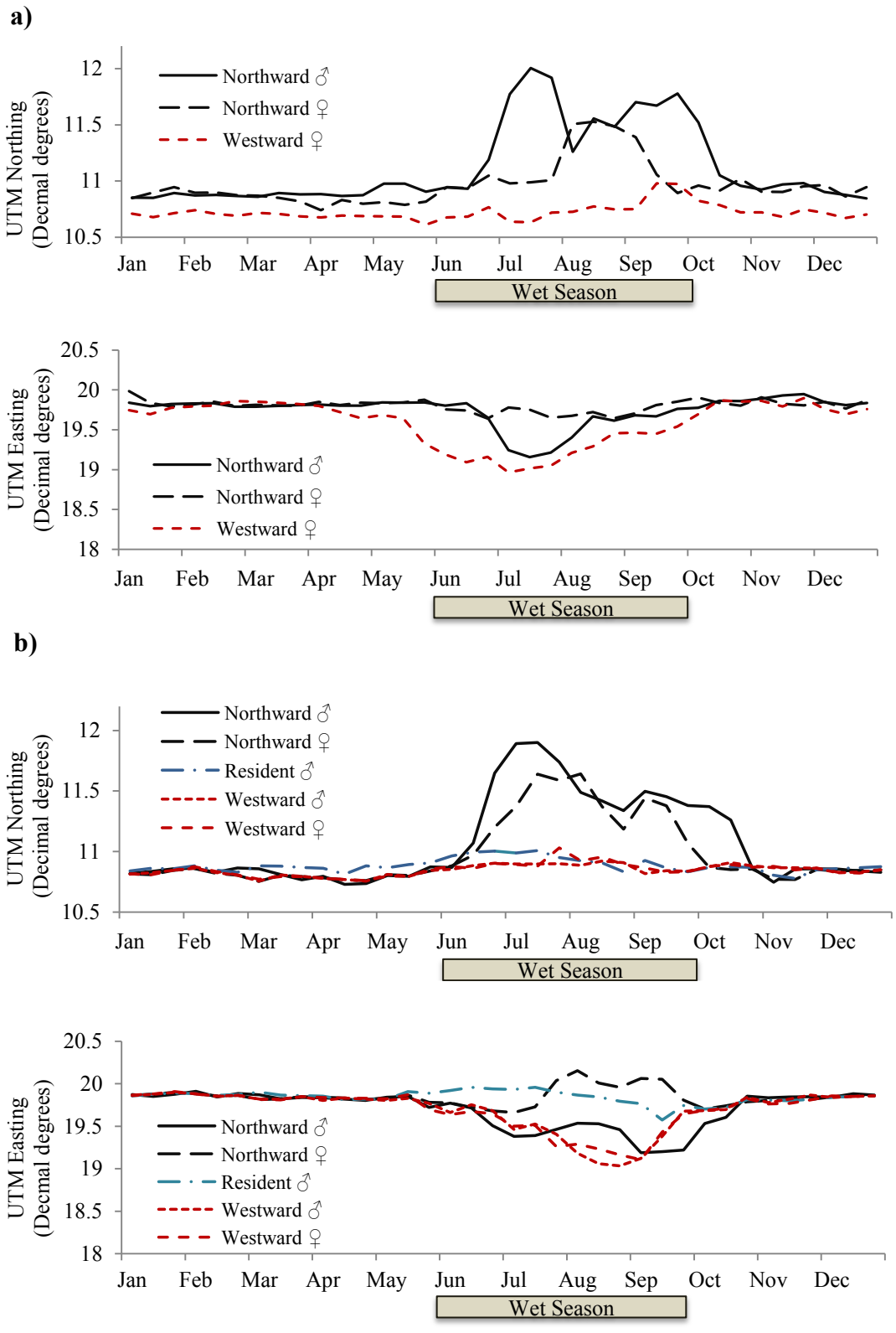

Fig. 3.2. *Average UTM Easting and Northing within ten-day time frames nested within months, with elephants grouped according to migration pattern, for satellite collared African elephants in Zakouma National Park from a) 2000 to 2003, and b) May 1, 2011 to April 30, 2013.*

The timing of the initiation of, and return from, northward and westward migrations is variable across years (Fig 3.3). The northward-migrating elephants moved out of the park before the westward-migrating elephants in both 2011 and 2012 (Fig 3.3). The initiation of both the westward migration and the northward migration took place after a similar amount of rain had fallen across years (northward migration ≈ 160 mm, westward migration ≈ 270 mm). The northward-migrating elephants returned to the park substantially earlier in 2012 than in 2011 (Fig. 3.3b). A splinter herd (± 23 animals including Z5A) from the main herd of northward-migrating elephants utilized an area in the western half of the northern range and returned much later than the majority of the northern herd, which inhabited the area around Fodjo swamp for the majority of the time spent outside of the park. One collared animal from the main northern herd was poached in the eastern half of the northern range circa August 10, 2012, and the elephants utilizing this area at the time returned to Zakouma National Park shortly after this incident. This return movement to Zakouma National Park took place earlier than in 2011 and took place over a month earlier than the return of the splinter herd of northward-migrating elephants (Fig. 3.3b).

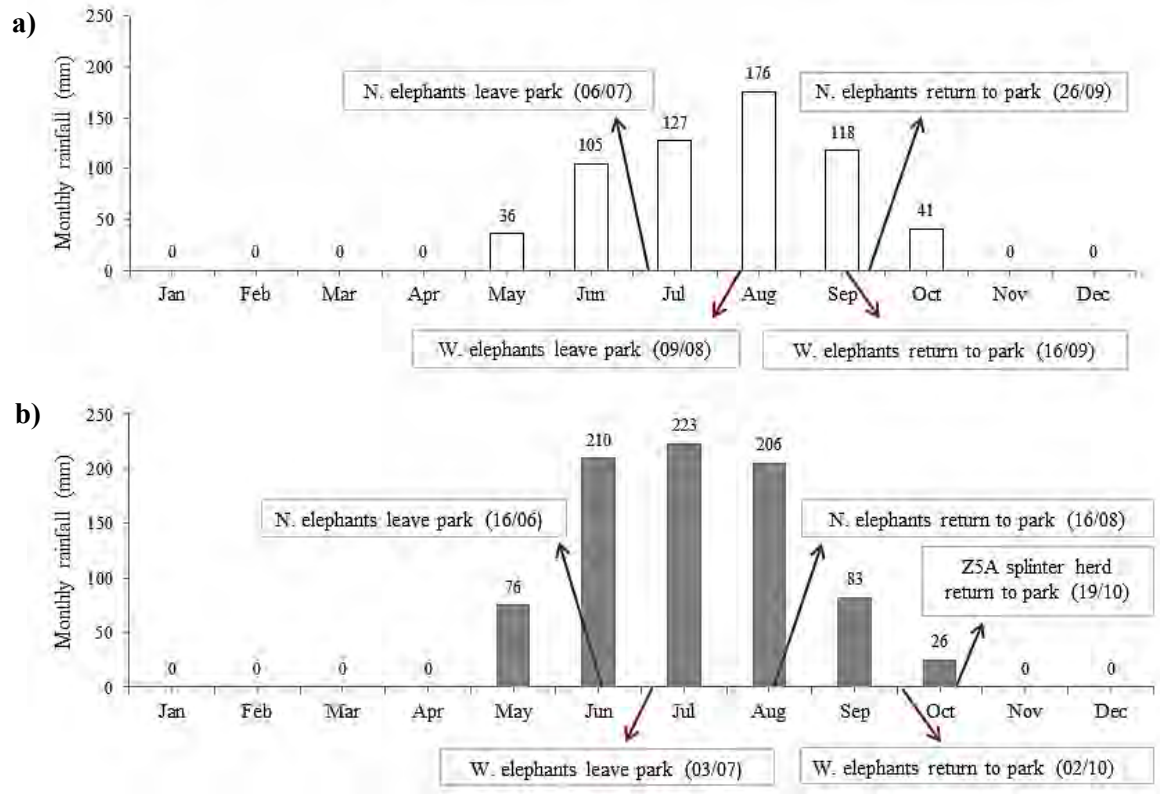

Fig. 3.3. *Monthly rainfall in combination with the timing of the departure from, and return to, Zakouma National Park, for northward and westward migrations, in a) 2011 and b) 2012.*

The transhumance population in the greater Zakouma ecosystem start moving away from their dry season settlements to the south and east of Zakouma National Park at the onset of the rainy season. In June their northward-movements are observed to intersect those of the northward- and westward-migrating Zakouma National Park elephants, in the areas to the north and west of the park (Fig. 3.4). The overlap between the areas utilized by the nomads is greater and occurs for a longer period of time to the north of the park (Fig 3.4). By the end of August the nomadic people are at the northern limit of the elephant population's wet season range. The transhumance population usually returns to the peripheries of Zakouma National Park in late September; however this is variable across years depending on annual rainfall patterns.

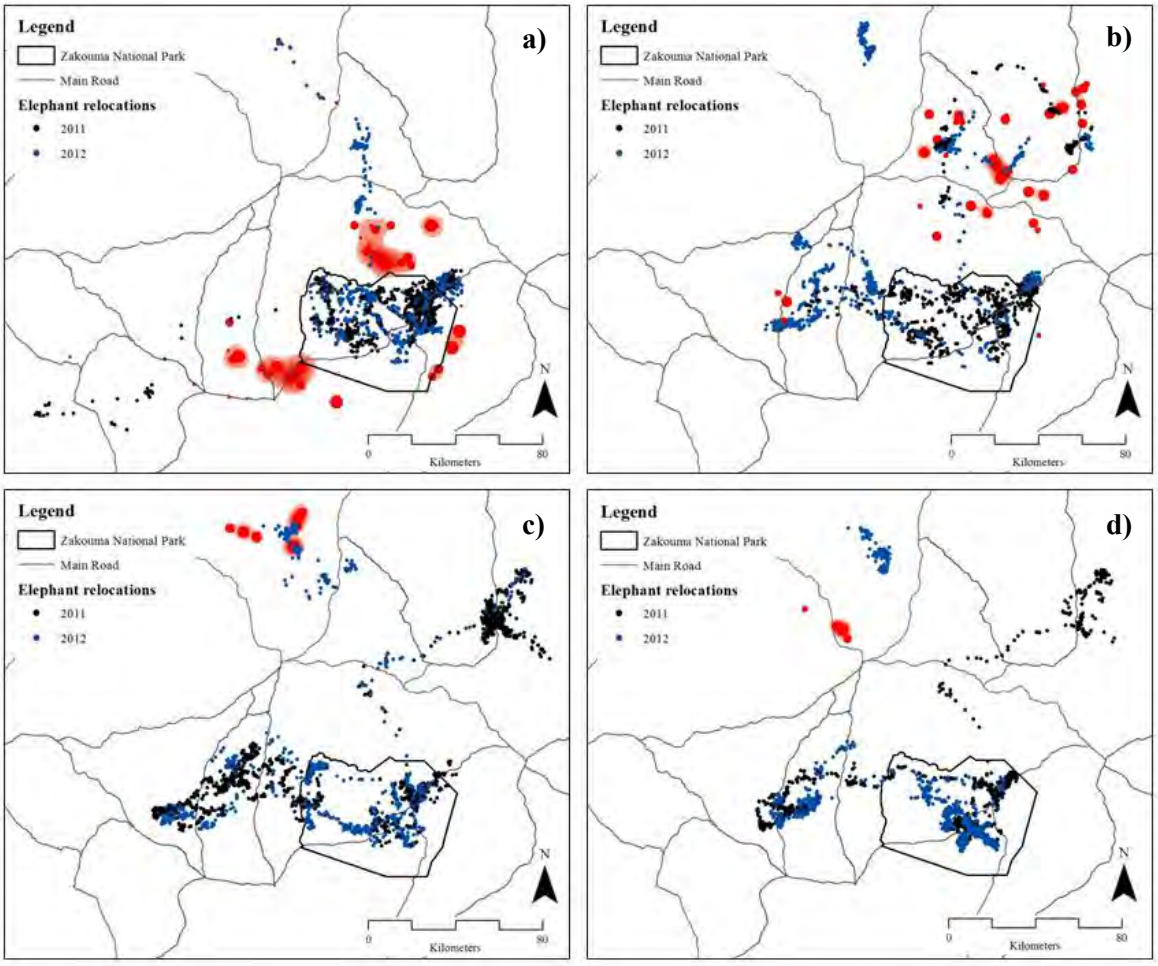

Fig. 3.4. *Observed elephant and transhumance population locations during a) June, b) July, c) August, and d) September. Transhumance locations were collected in 2011 while elephant relocations are for both 2011 and 2012. Red patches show the observed locations of the nomadic people of the area in 2011, with darker red areas indicating a higher density of observations and light red fewer observations.*

3.2. Movement behaviour

After inter-fix time intervals greater than 8.5 hours were removed, to mitigate the effects of the negative correlation between inter-fix movement speed and time interval, a total of 29 892 bridging segment observations remained for the thirteen study animals over the full study period (May 1, 2011 to April 30, 2013). Movement speed between successive GPS location fixes for all study animals over the full study period ranged between 0.0006 and 6.62 km/h (n=29 892). The maximum movement speed between subsequent elephant relocation positions observed for males was 6.43 km/h while for females the maximum was 6.62 km/h.

Table 3.1. *Mean (±SD) and maximum speeds travelled by groups of the elephants collared from May 1, 2011 to April 30, 2013 as well as the number of bridging segments used to calculate means (n).*

Group	Statistic	Inside Zakouma N.P.		Outside Zakouma N.P.	
		Day	Night	Day	Night
Northward-migrating	*Mean ± SD:*	0.56 ± 0.50	0.62 ± 0.55	0.46 ± 0.45	0.52 ± 0.76
	Max. speed:	3.82	4.12	3.43	6.62
	n:	4933	4461	1157	990
Westward-migrating	*Mean ± SD:*	0.57 ± 0.51	0.64 ± 0.60	0.63 ± 0.52	0.62 ± 0.83
	Max. speed:	4.60	4.41	3.62	5.93
	n:	6801	6036	1084	813
Resident bulls	*Mean ± SD:*	0.50 ± 0.44	0.53 ± 0.51	0.46 ± 0.34	0.56 ± 0.56
	Max. speed:	3.32	5.95	2.06	6.43
	n:	1544	1399	362	312

The generalised linear mixed effects models with speed as dependant variable had a significant location effect and period effect for both the westward- and northward-migrating elephants (Table 3.2), while the location by period interaction was only significant for the westward-migrating elephants (Table 3.2). For the resident bulls the location effect and the interaction between period and location were not significant, but there was a significant period effect (Table 3.2). The westward-migrating elephants moved significantly faster in the areas utilized outside of the park boundaries than within the park (Table 3.1, Table 3.3). In contrast to this the northward-migrating elephants moved significantly faster during the time spent within the park than in the areas utilized outside of Zakouma National Park (Table 3.1, Table 3.3).

Table 3.2. *Results of generalised linear mixed effects (GLMM) models fitted with speed as dependant variable and individual as random effect and the effect of location, daytime period and the interaction between these two factors as fixed effects, for satellite collared elephants grouped by migration (northward-migrating, westward-migrating, resident bulls). Degrees of freedom are not calculated for GLMMs fitted using the "lme4" package in RStudio (Bolker et al. 2008).*

	Parameter estimates (B_i)	Standard Error	*t*	*P*
Northward-migrating elephants (11 541 observations for five individuals)				
(Intercept)	1.80	0.049	36.73	$P < 0.0001$
location	0.36	0.066	5.50	$P < 0.0001$
period	-0.17	0.033	-5.07	$P < 0.0001$
Location : period	0.06	0.091	-0.65	$P = 0.52$
Westward-migrating elephants (14 734 observations for six individuals)				
(Intercept)	1.81	0.055	32.81	$P < 0.0001$
Location	-0.15	0.050	-3.04	$P = 0.0024$
Period	-0.20	0.028	-7.35	$P < 0.0001$
Location : period	0.20	0.075	2.67	$P = 0.0076$
Resident bulls (3 617 observations for two individuals)				
(Intercept)	2.21	0.21	10.28	$P < 0.0001$
Location	0.18	0.11	1.70	$P = 0.090$
Period	-0.13	0.063	-2.14	$P = 0.03$
Location : period	-0.26	0.15	-1.78	$P = 0.075$

All groups of elephants moved significantly faster at night than during the day (Table 3.1, Table 3.3). However, there was a significant location by period interaction for the westward-migrating elephants, with no significant difference in nocturnal and diurnal movement speeds in the wet season home-range to the west of Zakouma National Park (Table 3.1, Tukey post hoc comparison: $Z_{(1\,897)} = 0.025$, $P = 1.00$) and significantly faster nocturnal than diurnal movements within the park (Table 3.1, Tukey post hoc comparison: $Z_{(12\,837)} = 7.35$, $P < 0.0001$). The northward- and westward-migrating elephants behaved differently in terms of nocturnal and diurnal movement speed in their wet season home-ranges, outside of the Zakouma National Park boundaries, although similar movement behaviour was observed for these two groups within the park boundaries (Table 3.1). The westward-migrating elephants had a higher rate of displacement in their wet season range, to the west of the park, while the opposite was observed for the northward-migrating elephants (Table 3.1, Table 3.3). The study elephants that utilized the area to the north of the park were however more active at night than during the day outside of

the park boundaries (Table 3.1, Table 3.3). The satellite collared elephants observed to migrate to the west of the park showed no significant difference in day and night time activity in their wet season home range (Table 3.1, Table 3.3).

Table 3.3. *Results of Wald chi-squared test for the location and period effect, as well as the location by period interaction, for each group of satellite collared elephants. Bold text results are those which were significant at $P < 0.05$.*

Factor or interaction	Northward-migrating	Westward-migrating	Resident bulls
Location	**$\chi^2_{(1)} = 30.28$, $P < 0.0001$**	**$\chi^2_{(1)} = 9.24$, $P = 0.002$**	$\chi^2_{(1)} = 2.88$, $P = 0.090$
Period	**$\chi^2_{(1)} = 25.75$, $P < 0.0001$**	**$\chi^2_{(1)} = 54.06$, $P < 0.0001$**	**$\chi^2_{(1)} = 4.58$, $P = 0.032$**
Location : period	$\chi^2_{(1)} = 0.42$, $P = 0.52$	**$\chi^2_{(1)} = 7.12$, $P < 0.008$**	$\chi^2_{(1)} = 0.42$, $P = 0.075$

Monthly movement speeds for each group of study animals increased with an increase in upper mean temperature from the start of the hot dry season in February to the onset of the wet season in late May to early June (Fig. 3.5). The maximum monthly movement speeds for the westward- and northward-migrating elephants were observed in May (westward-migrating: 0.74 ± 0.69 SD km/h, northward-migrating: 0.73 ± 0.69 SD km/h) and June (westward-migrating: 0.82 ± 0.72 km/h, northward-migrating: 0.73 ± 0.67 km/h) while for the resident bulls the highest mean monthly movement speed was observed in September (0.61 ± 0.50 km/h). Movement speeds were particularly low for the northward-migrating elephants in July, August and September, the period spent in the northern wet season home-range. At a monthly temporal scale nocturnal movement speeds became increasingly faster in comparison to diurnal movement speeds as the dry season became hotter and drier (Fig. 3.5). Nocturnal movement speeds were faster than diurnal movement speeds in the wet season months of June and July for both the westward- and northward-migrating elephants (Fig. 3.5a, Fig 3.5b). This coincides with the general timing of elephant dispersal out of the park into the wet season home-ranges to the north and west of the park. Differentiation of nocturnal and diurnal movement behaviour was less pronounced for the resident bulls (Fig. 3.5c).

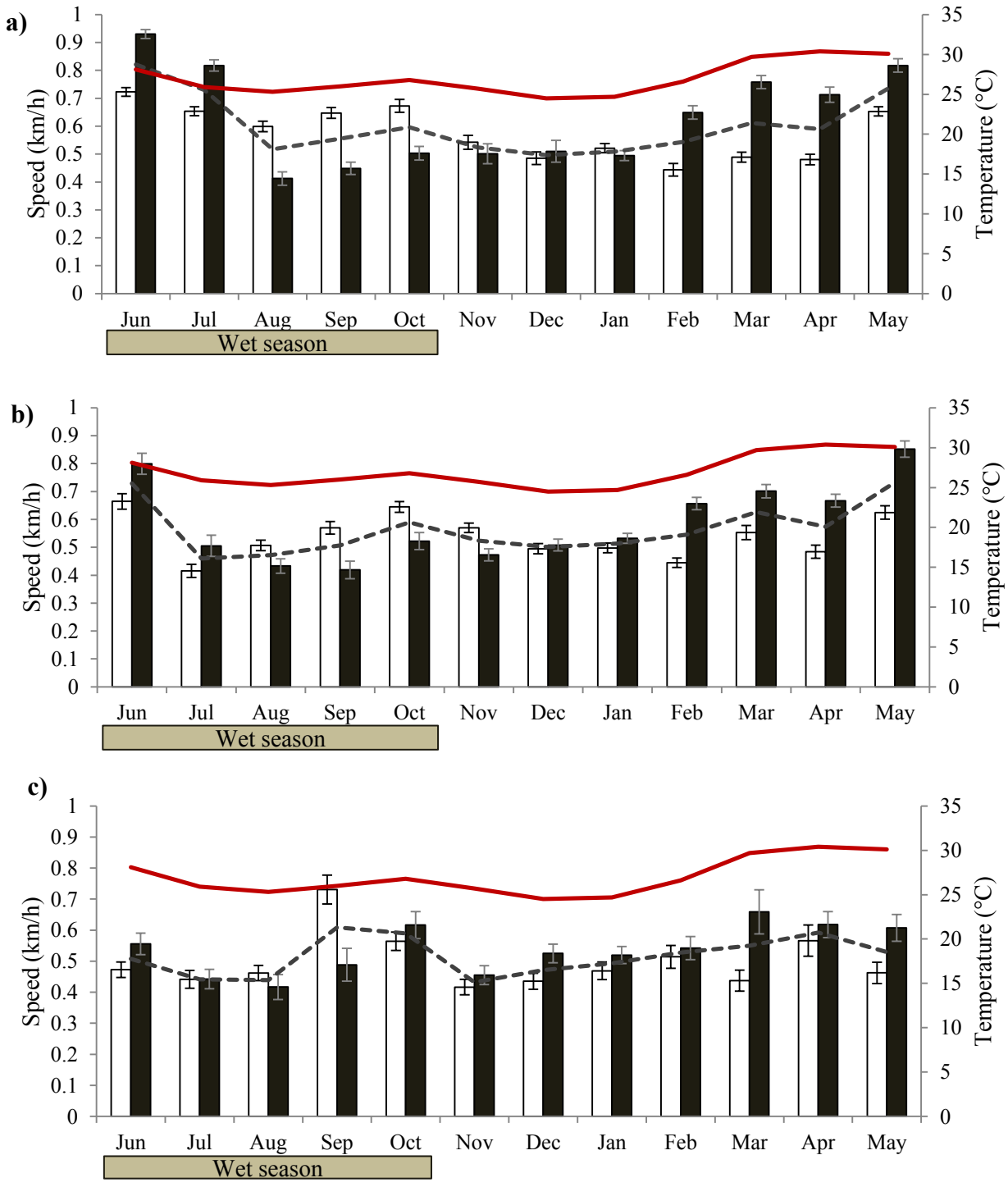

Fig. 3.5. *Mean (± SE) diurnal (white bars) and nocturnal (shaded bars) movement speeds of a) westward-migrating elephants, b) northward-migrating elephants and c) resident bulls in Zakouma National Park in combination with upper mean monthly temperature represented by a solid red line (Dejace 2002). Average monthly movement speeds within each group of elephants are represented by the dashed line.*

The upper limit of the 5th, 25th, 50th, 75th and 95th percentiles of mean movement speed within the grid squares utilized by the study animals, over the full study period, were 0.40, 0.74, 1.61, 3.78, and 7.0 km/h respectively (Fig. 3.6a). The upper limit of the mean turning angle within each grid square for the same sequence of percentiles was 10.76, 46.79, 83.04, 109.13, and 180 degrees respectively (Fig. 3.6b). Movement behaviour was positively spatially auto-correlated in terms of both speed and turning angle, across the wet and dry season (Table. 3.2). During the wet season there was a higher prevalence of higher than normal and lower than normal movement speeds and turning angles in the areas utilized outside of Zakouma National Park (Fig. 3.7). Furthermore, the patchy distribution of faster than normal and slower than normal movement speeds was more pronounced in the areas to the north and west of Zakouma National Park than within the park boundaries (Fig. 3.7). Likewise the distribution of more directed than average and less directed than average movements formed defined patches in the areas utilized outside of Zakouma National Park (Fig. 3.7). Within the park mean movement speed and turning angle per grid square was predominantly indicative of average movement behaviour. Positive spatial autocorrelation was more pronounced for mean movement speed than turning angle, and both speed and turning angle were more spatially autocorrelated during the wet season than in the dry season (Fig. 3.8, Table 3.4).

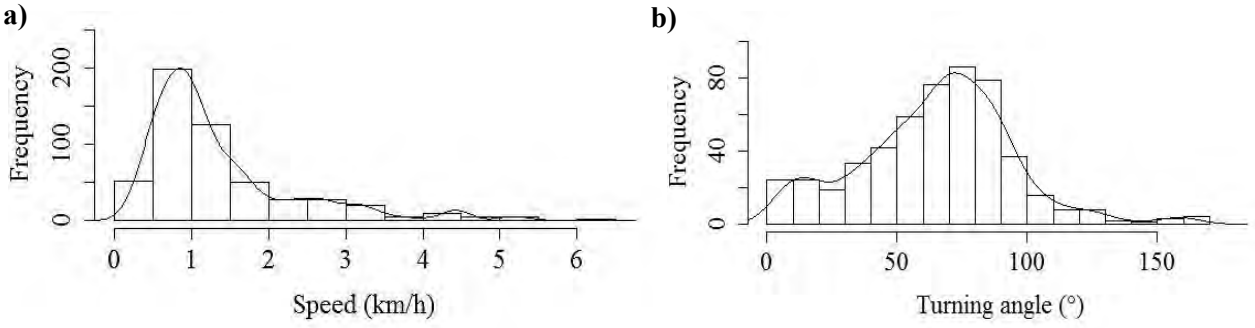

Fig. 3.6. *Histograms showing the distribution of a) mean speed per grid square and b) turning angle per grid square for the movement behaviour raster.*

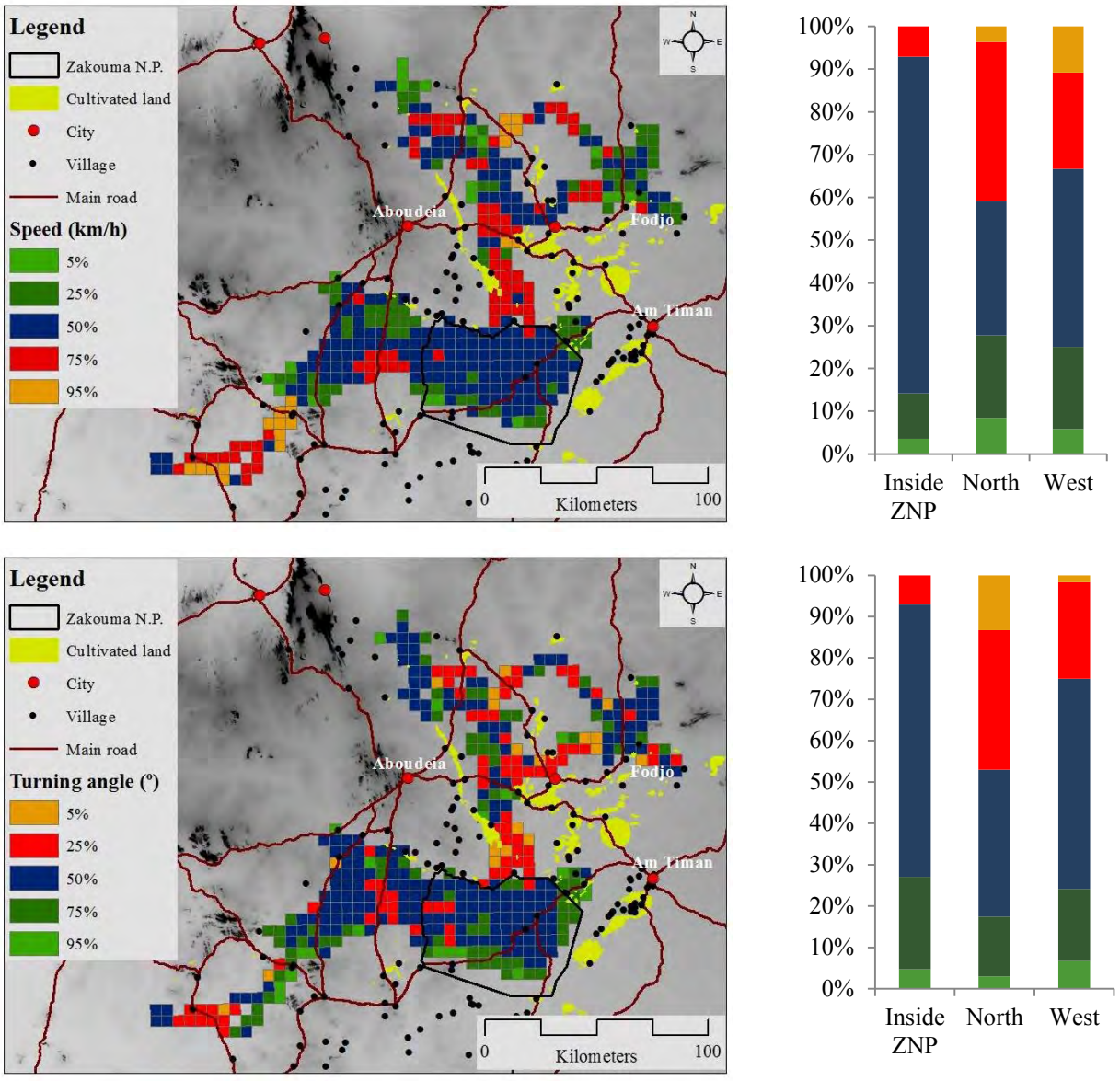

Fig. 3.7. *Maps showing the distribution of categories of movement speed and turning angle within 25 km^2 grid-squares in the areas utilized by the Zakouma National Park (ZNP) elephant population during the wet season. Bar graphs show the proportion of each category of movement behaviour, in terms of speed and turning angle, in clusters of grid squares grouped according to location. Blue grid squares indicate areas within which average movement speeds and turning angles were observed. Dark green grid squares are indicative of movements that are at a slower than average speed and are more tortuous than average movements, while red grid squares indicate movements that are faster than average movement speeds and are more directed than average movements. Light green grid squares indicate areas in which the slowest movements and the most tortuous movement paths were observed, while orange grid squares indicate areas of the highest movement speeds and most directed movement paths. The location of major roads, villages and cultivated land in the area are additionally shown.*

A large contiguous patch of fast, directed movement was observed in the area between the Zakouma National Park boundary and the wet season home-range to the north of the park (Fig. 3.7). The area bridged by this migration corridor is characterised by a high prevalence of human presence (Fig. 3.7), and furthermore there are no permanent water sources in this area. The busiest road crossed by the elephants in the Zakouma ecosystem is the main road between Aboudeia and Am Timan, which links this region to the capital city, N'Djamena. The grid squares intersected by this road were characterized by swift movements (Fig. 3.7). Grid squares intersected by other main roads in the areas to the north and west of the park, were also characterised by fast, and directed movements (Fig. 3.7). The movement behaviour observed in over forty percent of grid squares within the northern wet season home-range was indicative of fast movements and directed movement paths (Fig. 3.7).

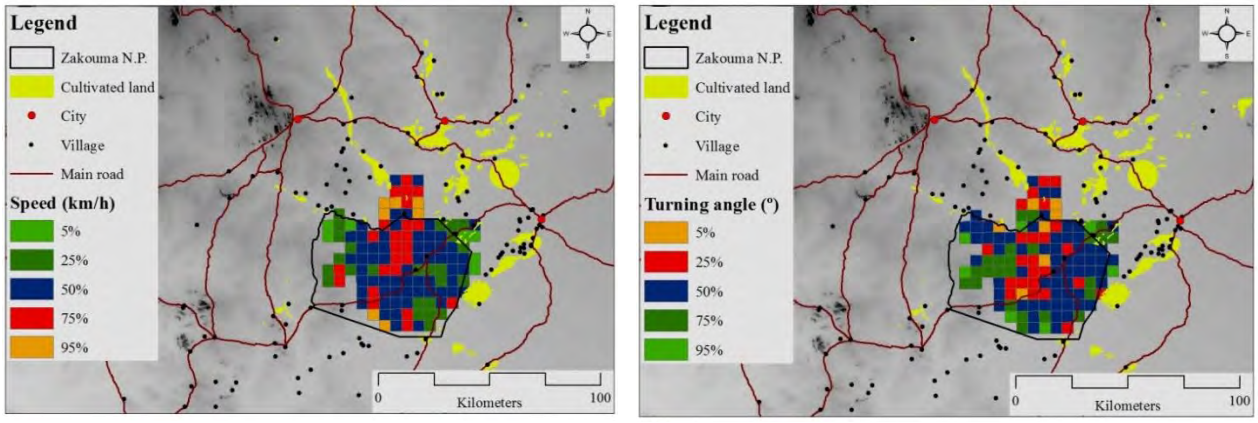

Fig. 3.8. *Maps showing the distribution of categories of movement speed and turning angle within 25 km^2 grid-squares in the areas utilized by the Zakouma National Park elephant population during the dry season.*

In the areas to the north of the park some grid squares and patches of grid squares with slow movement speeds and tortuous movement paths were surrounded by contrasting fast and directed movements, while within the park and to the west of the park this pattern was less apparent (Fig. 3.7). The small patches of slow, tortuous movements within larger patches of movement behaviour indicative of stress (fast and directed) may represent refugia, while the larger patches of slow tortuous movements, within patches of normal movement behaviour, are most likely areas containing favourable resources (Fig. 3.7). During the dry season, when movement is restricted by the distribution of water, contrasting movement behaviour was less patchily

distributed (Table 3.4, Fig 3.8). However, a contiguous patch of swift, directed movements was observed in the western half of the park (Fig 3.8). Few water resources persist in this area during the dry season, which may account for this movement behaviour. During the dry season swift, directed movements additionally took place through grid squares located outside of Zakouma National Park (Fig. 3.8).

Table 3.4. *Moran's I statistic for mean speed and turning angle values of grid squares covering the area utilized by the Zakouma National Park elephant population during the wet season and the dry season.*

Movement metric	Moran's I	Standard Deviation	Significance (positive spatial autocorrelation)
Wet season:			
Speed (km/h)	0.14	0.0044	Sig. ($p < 0.0001$)
Turning angle (°)	0.072	0.0044	Sig. ($p < 0.0001$)
Dry season:			
Speed (km/h)	0.086	0.0086	Sig. ($p < 0.0001$)
Turning angle (°)	0.052	0.0088	Sig. ($p < 0.0001$)

4. Discussion

4.1. Movement pattern

At a coarse spatial and temporal scale the movement patterns of the Zakouma National Park elephant population show little change from 2000 to 2013 despite a decade of intensive poaching, and the resultant reduction of the population to a tenth of its former size. The migration patterns observed by Dolmia (2004) a decade earlier have not changed dramatically since the population became reduced to a tenth of its former size, however the lack of migration out of the park after the cut off period of this study suggests that the behaviour of this population is changing and should be carefully monitored. The consistency of the annual south-north and east-west movements carried out by the majority of this elephant population, at the onset of the wet season, now and at a time when the population was much larger indicates that environmental heterogeneity through space and time is the key driver of this migration. Through the insights gained from movement ecology studies in similar environments elsewhere in Africa, in combination with observations on the ground in Zakouma, two main hypotheses are put forward to explain the wet season elephant movements away from the eastern half of the park. These are as follows, (i) movements are driven by pulses in verdancy of high quality vegetation in the areas to the west and north of the park, and (ii) migrations occur as a means of escaping the flooding that takes place in the lower lying dry season range of this population.

Elephants in the Gourma region in Mali carry out a seasonal migration in the opposite direction to the Zakouma National Park elephants, with southward movements initiated at the onset of the wet season (Wall et al. 2013). A study of the vegetation in the Malian Sahel found that at the northern limit of the Sahel water is the major limiting factor of plant growth, resulting in seasonal pulses of high quality forage in these areas (Breman & De Wit 1983). Further south in the Sahel plant growth was found to be limited by important nutrients rather than water, resulting in high plant biomass but lower plant quality (Breman & De Wit 1983). It has been suggested that the Gourma elephant migration is driven by temporary selection for areas containing a higher biomass of plant matter, as opposed to selection for high quality resources (Wall et al. 2013). Furthermore, this population is restricted to the northern section of their range, within which the permanent water sources of the region are found, during the dry season (Wall et al.

2013). In contrast to the conditions in the Gourma region, important dry season water sources are found within Zakouma National Park in the southern and eastern extent of the observed range of the northward- and westward-migrating Zakouma elephants respectively. The difference in the location of important dry season water sources within the home-ranges of these two elephant populations may impose contrasting migration patterns in response to the distribution of resources in Gourma and Zakouma.

A similar south-north gradient of plant quality to that observed in Mali may be a driver of the northward elephant migration observed in Zakouma during the wet season, when rainfall reduces the constraints of water availability, allowing short term growth pulses of high quality vegetation in the northern extent of the Zakouma National Park elephant range. Following this logic, the movement pattern of the Zakouma National Park elephants is more consistent with the search for limiting nutrients described in ungulate migration systems in east Africa (Holdo et al. 2009) than the elephant movements towards areas with a higher plant biomass observed in the Gourma region in Mali (Wall et al. 2013). The movements to the west and south-west of the park are not explained by this hypothesis and may be regulated by the distribution of specific plant species or mineral resources (Douglas-Hamilton et al. 2005, Wall et al 2013). Elephants are however generalist in their diet choice, and are furthermore observed to select for open shrub lands and herbaceous vegetation on flooded areas, during the wet season in other seasonally variable ecosystems, and show a preference for grass over browse during this time (Loarie et al. 2009, Lindsay 2011, Pittiglio et al. 2012). The movement of the Zakouma elephants away from an area characteristic of the wet season preferences of other elephant populations suggests that other interacting factors play a role in shaping the Zakouma National Park elephant migration.

Movements out of the national park for both northward- and westward-migrating elephants took place about a month earlier in 2012 than in 2011 and the initiation of these movements occurred after about 160 mm and 270 mm of rain had fallen for the northward- and westward-migrating elephants respectively. This may be due to elephant movements depending on the replenishment of ephemeral water sources along migration routes (Western & Lindsay 1984, Wall et al. 2013). Alternatively, the northward and westward migrations carried out by the Zakouma elephants may be driven by the avoidance of flooding in the lower-lying eastern half of the park during the wet season. Elephants have been found to avoid flooded areas during wet season migrations in the

Tarangire-Manyara ecosystem in Tanzania (Pittiglio et al. 2012). The location of water is an important determinant of the spatio-temporal organisation of elephants during the dry season, especially in highly variable semi-arid ecosystems (de Beer & Van Aarde 2008, Wall et al. 2013), but may be a further determinant of elephant distribution during the wet season through the avoidance of flooded areas.

The transience of the availability of water during the dry season results in the elephant population becoming concentrated in the eastern half of Zakouma National Park, anchored by the few permanent water sources remaining in this area. The areas to the south and east of the park also maintain water sources for the full extent of the dry season; however these water sources, situated outside of the park boundaries, attract high concentrations of pastoralists and their livestock at this time of year. The absence of observed movements to the south of Zakouma National Park, during the dry season, between 2011 and 2013 may be a result of the decrease in elephant numbers and the resultant reduced intra-specific competition, allowing the eastern section of the park to support the entire elephant population for the full dry season period. Alternatively, an increase in human population on the periphery of the park may constrain dry season movements into this area. Elephants face competition with livestock and people at water sources outside of protected areas (Wittemyer et al. 2007, Wall et al. 2013), and thus movements outside of the park during the dry season when this would be the case are avoided. This is a strong possibility in this area, especially during the dry season when the transhumance population of the area occupies the areas to the south and east of Zakouma National Park, resulting in a higher chance of human-elephant conflicts at water sources at this time.

Both conjectures put forward to explain the northward and westward wet season migrations of the Zakouma elephants are supported by the similarity in the spatio-temporal movement patterns of the transhumance population and the elephant population in this region, as well as the clear initiation of these movements at the onset of the rains. A social study on the dynamics and reasons for the movement patterns of the transhumance population of this area would be of value to understanding the drivers of their movements and possibly those of the elephants. Due to the similarity between the movements of these people and the Zakouma elephants, tapping into the knowledge of an ancient culture of migrating people could provide valuable information on the processes underlying migration in this system. Although a detailed vegetation map exists for

Zakouma National Park information about the vegetation to the north and west of the park, as well as the gradients of vegetation quality across the areas utilized by the Zakouma elephants are depauperate. Further studies would benefit from the inclusion of information on the nutritional quality and greenness of vegetation in different areas through the Zakouma elephant range, as well as seasonal variability in greenness, in order to explore patterns of selection for different vegetation types at different times of the year. Furthermore field observations of elephant diet choice within dry season and wet season home-ranges may provide additional information on the selection for specific plant species located in different areas. Data on the level of inundation in different areas through the Zakouma elephants' range may give insight into whether elephants avoid highly flooded areas. Due to a lack of data on these important environmental factors, the drivers of elephant movement patterns were not explored and are thus an important aspect of the movement ecology of this population to be studied further.

4.2. Movement behaviour

At a finer spatial and temporal resolution shifts in movement pattern have occurred over the past ten years and movement behaviour indicative of human induced stress has emerged in the areas utilized outside of Zakouma National Park. It is becoming increasingly clear that elephant movement behaviour is variable across seasons and in different areas within elephant home-ranges (Douglas-Hamilton et al 2005, Galanti et al. 2006, Graham et al. 2009, Wall et al. 2013). During the dry season food and water resources become patchily distributed, and elephant movements are restricted by the distribution of water during this period (Galanti et al. 2006, Leggett 2006, Pittiglio et al. 2012). In line with this, the area utilized by the Zakouma National Park elephants during the dry season was much smaller than the area through which they dispersed during the wet season, when food and water resources are abundant. During the dry season in semi-arid regions in Kenya elephant family unit cohesion has been found to decrease as a result of intraspecific competition (Western & Lindsay 1984, Wittemyer et al. 2005). In contrast to this, the Zakouma National Park elephant population are observed to congregate during the dry season, when the elephant population is concentrated in the eastern half of the park. During this time variation in nocturnal and diurnal movement speeds became pronounced, and the increase in nocturnal movement speed was correlated with the increase in upper mean-temperature and the duration of the dry season.

Elephants are active both during the day and at night, but tend to rest during the heat of the day (Leggett 2009). During the hottest months of the dry season the Zakouma National Park elephant population rests for much of the day, with extended periods of time spent stationary, in the shade of trees (Fig. 4.1). Rapid nocturnal relocations to water sources or new feeding grounds are thus expected to take place at night during this time, as a strategy to avoid heat exhaustion (Leggett 2009, Dunkin et al. 2013). During the wet season when resources are abundant elephants are observed to disperse over large areas and generally exhibit a high rate of displacement and variability in movement behaviour during this period (Harris et al. 2008, Loarie et al. 2009, Birkett et al. 2012). The migrating elephants in the Zakouma National Park population move into human-occupied landscapes at the onset of the wet season, where the majority of the wet season months are spent. During this time contrasting movement behaviour arose for the elephants that disperse to the areas to the north and the west of the park, although these elephants behave similarly within the park boundaries, during the dry season.

There are markedly fewer human settlements and less agricultural development in the areas to the west of Zakouma National Park than to the north of the park. The higher movement speed observed for the westward-migrating elephants in the areas utilized outside of Zakouma National Park, may be explained by seasonal variation in movement behaviour, as the time spent outside of the park boundaries largely corresponds with the wet season. The contrasting slower movement speed, and increased nocturnal activity exhibited by the northward-migrating elephants in their wet season home-range indicates that factors other than seasonal variability in resource availability play a role in shaping the movement behaviour of elephants in this area. Elephants have been found to carry out swift movements under the cover of darkness when moving through human-dominated landscapes as a mechanism of avoiding human encounters (Galanti et al 2005, Douglas-Hamilton et al. 2005, Graham et al. 2009, Kangwana 2011, Granados, Weladji & Loomis 2012). The higher degree of nocturnal activity in relation to diurnal activity observed in the area to the north of Zakouma during the wet season, and the lack of these differences to the west of the park suggest that this behaviour may be a human avoidance strategy employed in the northern wet season home-range.

Fig. 4. *Photograph showing shade-seeking behaviour by the Zakouma National Park elephants during the heat of the day in the hot dry season (circa. April 2011). Photo courtesy Warren Steyn.*

The grid-square approach employed to classify discrete areas according to movement behaviour provides an indication of the spatial distribution of different movement behaviours during the wet season and the dry season. During the wet season, when extensive movements outside of Zakouma National Park take place, a large contiguous patch of fast, directed movement behaviour, corresponding with the location of the corridor linking the park to the northern wet season home-range, was observed. The adoption of this 'streaking' behaviour implies that elephants perceive danger when moving through this area (Douglas-Hamilton et al. 2005, Jachowski et al. 2013b). In light of this observation the northern migration may soon come up against anthropogenic barriers to dispersal. A patch of fast movement speeds and to a lesser extent directed movement paths, corresponded with the intersection of the northward-migrating elephants' dispersal and the main road between Aboudeia and Am Timan. The amount of traffic on the roads in the greater Zakouma ecosystem is highly variable, with some roads seeing very little traffic. The road between Aboudeia and Am Timan is the most heavily utilized in the area as it is the main route of transport between the capital, N'Djamena, and this region. Furthermore,

the two patches of the highest movement speed category to the west of the park and the largest patch of this movement behaviour to the north of the park were all intersected by roads. These findings are in line with road response behaviour exhibited by the Gourma elephants (Wall et al. 2013) as well as that recorded for *Loxodonta africana cyclotis* in north-eastern Gabon (Barnes 2008). The road between Aboudeia and Am Timan is currently not tarred and traffic in this remote region is most likely less than that experienced in certain wildlife areas in Kenya (Pinter-Wollman 2012) and Cameroon (Granados, Weladji & Loomis 2012) where highways have been found to form barriers to elephant movement. Nevertheless, this road intersects the northern wet season range of the Zakouma National Park elephant population and has the potential to cut off the important elephant dispersals into this region.

Small patches of slow, tortuous movements within larger patches characterized by swift, directed movements were additionally observed in the wet season range to the north of Zakouma National Park. This pattern is characteristic of refuge behaviour whereby elephants exposed to a perturbation or stress actively seek out refugia within patches of dense vegetation as an avoidance mechanism (Jachowski et al. 2012). Swift movements through corridors, often under the cover of darkness, occur between these refugia in areas where elephants perceive danger (Douglas-Hamilton et al. 2005, Jachowski et al. 2013b). Studies carried out on chronically stressed, relocated elephants in southern Africa found that these elephants exhibited restricted space use and adapted their behaviour and habitat preferences resulting in extended stays within areas of dense vegetation (Jachowski et al. 2012). Furthermore, in the Gounda-St Floris National Park in Central African Republic the elephant population were observed to adapt their behaviour in response to high stress levels caused by poaching (Ruggiero 1990). Similar to the situation in Zakouma National Park, poachers in this area operated on horseback and generally assailed by day (Ruggiero 1990). This resulted in a shift in elephant behaviour in this park with extended diurnal stays in woodlands and dispersive foraging movements undertaken by night (Ruggiero 1990). The elephants in the Zakouma National Park ecosystem have been hunted for centuries, initially by the nomadic tribes of the region (Temporal 1989), and at present more commonly by disbanded rebel groups and soldiers from conflicts in the politically unstable neighbouring countries of Sudan and the Central African Republic. The presence of small patches of confined elephant movement behaviour in the areas to the north of Zakouma National Park may be due to

the adoption of a similar refuge-seeking behavioural strategy by the Zakouma elephants, in the presence of humans, in order to avoid the elephant's primary predator: man.

The Zakouma National Park elephants adopt behaviour indicative of human-induced stress in the areas outside of the park and this behaviour is more pronounced to the north of the park than to the west. This study did not explore the effects of interacting environmental and anthropogenic attributes on movement behaviour. A model exploring these interactions would provide more detailed insight into the relationship between movement behaviour and anthropogenic influence in combination with environmental conditions. Furthermore combining the distribution of speed and turning angle data would be beneficial in order to delineate areas of fast and directed movements. During the wet season of 2013, after the telemetry data cut-off time for this study, the Zakouma National Park elephant population did not carry out wet season migrations outside of the park boundary. This shift in migration behaviour necessitates the continued study of the movement ecology of this elephant population.

4.3. Synthesis and management recommendations

The distribution of important and favourable resources is the major process that determines elephant movements and distributions in Africa (Harris et al. 2008, de Boer et al. 2013). However, human influence is becoming an increasingly important predictor of both elephant distributions and the movement behaviour they exhibit in different areas (Douglas-Hamilton et al. 2005, de Boer et al. 2013). If elephant migrations out of Zakouma National Park are to continue, some form of land-use planning should be carried out for the areas to the north and, to a lesser extent, to the west of Zakouma National Park. Although the adoption of a rigorous anti-poaching campaign in this ecosystem has dramatically reduced poaching, the loss of important habitat outside of Zakouma National Park remains a worrying threat to the recovery of this elephant population. The maintenance of migration corridors is of particular importance in order to maintain connectivity between the park and the areas utilized to the north of the park. The findings of this study suggest that the boundaries of the Bahr Salamat Faunal Reserve, or those of Zakouma National Park itself, should be re-aligned to include important elephant dispersal areas. Poverty, a lack of basic civil structure and the stochastic environmental and political conditions experienced by communities on the periphery of Zakouma National Park require

conservation planning that is compatible with both livelihoods of the people of this area, and conservation and land use planning objectives.

Accommodating the needs of local people and attracting foreign exchange through sustainable use of wildlife may be particularly challenging in this remote area stigmatized by political insecurity and war. Furthermore, with the successful protection of elephants and a growing human population, an increase in human-wildlife conflict can be expected. In the face of these multi-dimensional challenges it is important that both the ecological and social implications of management actions are investigated, preferably with the engagement of relevant stakeholders. However, due to the 'crisis-discipline' nature of conservation biology (Soulé 1985) these decisions must be made with some urgency. Management decisions should thus be carefully monitored and in the case of negative ecological or socio-economic results, should be adapted accordingly.

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Appendix 1. *Additional information for the 2011-13 study animals, outlining collaring location and date, tracking duration and duration of different inter-fix intervals.*

ID	Collaring date	Collaring co-ordinates		Sex	Age	Seasonal migration	Inter-fix time interval:			Tracking duration	Additional information
		Latitude	Longitude				1 hour	4 hours	8 hours		
Z1	21/04/2011	10.94545	19.95256	M	15-19	Resident	01/05/2011-06/05/2011	06/05/2011-06/05/2012	06/05/2012-11/04/2011	01/05/2011–11/04/2011	Collar stopped working 11 April 2013
Z2	22/04/2011	10.83206	19.83745	F	13-15	North	01/05/2011-06/05/2011	06/05/2011-06/05/2012	06/05/2012-30/04/2013	01/05/2011-30/04/2013	Collar malfunctioned July & August 2011
Z3	23/04/2011	10.82598	19.85642	F	10-11	West	01/05/2011-06/05/2011 and 07/11/2011 - 17/11/2011	06/05/2011-07/11/2011 and 17/11/2011-06/05/2012	01/05/2011-30/04/2013	01/05/2011-30/04/2013	
Z4	23/04/2011	10.83467	19.87227	M	17-19	West	01/05/2011-06/05/2011	06/05/2011 - 22/05/2012	22/05/2012 - 30/04/2013	01/05/2011-30/04/2013	
Z5A	23/03/2012	10.81405	19.85273	M	10-15	North	-	01/05/2012 - 23/04/2013	-	01/05/2012 - 23/04/2013	Refurbished collar, no interruption in service
Z6	24/04/2011	10.81742	19.85908	F	19	North	01/05/2011-06/05/2011	06/05/2011-30/04/2012	-	2011/05/01 2012/04/30	Poached ±10/08/2012
Z7	28/04/2011	10.70250	19.79400	M	19	West	01/05/2011-06/05/2011	06/05/2011-30/04/2013	-	2011/05/01 - 2013/04/30	
Z8	26/04/2011	10.83549	19.86197	M	15	West	01/05/2011-06/05/2011	06/05/2011-06/05/2012	06/05/2012-30/04/2013	2011/05/01 - 30/04/2013	
Z10	22/04/2011	10.83724	19.80318	F	10-14	North	01/05/2011-06/05/2011	06/05/2011-30/04/2013	-	01/05/2011-30/04/2013	

ID	Collaring date	Collaring co-ordinates		Sex	Age	Seasonal migration	Inter-fix time interval:			Tracking duration	Additional information
		Latitude	Longitude				1 hour	4 hours	8 hours		
Z11	19/03/2012	10.79246	19.74817	F	18	West	-	01/05/2012 - 2013-04-30	-	01/05/2012 - 2013-04-30	
Z12	16/03/2012	10.99412	19.94161	M	16	Resident	-	01/05/2012 - 06/05/2012	06/05/2012 - 30/04/2013	01/05/2012 - 30/04/2013	
Z13	22/03/2012	10.82717	19.86719	M	18	North	-	01/05/2012 - 30/04/2013	-	01/05/2012 - 30/04/2013	
Z15	31/3/2012	10.81493	19.86288	F	15-20	West	-	01/05/2012 - 06/05/2012	07/05/2012 - 30/04/2013	01/05/2012 - 30/04/2013	